STRUCTURE IN VITAL RATES, INTERNAL SOURCE-SINK DYNAMICS, AND THEIR INFLUENCE ON CURRENT POPULATION EXPANSION FOR THE FERAL HORSES (*Equus ferus caballus*) OF SABLE ISLAND, NOVA SCOTIA

A Thesis Submitted to the College of

Graduate Studies and Research

in Partial Fulfillment of the Requirements

for the degree of Master of Science

in the Department of Biology

University of Saskatchewan

Saskatoon

By

Adrienne Louise Contasti

PERMISSION TO USE

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission or copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor who supervised my thesis work or, in their absence, by the Head of the Department or the Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

_____

Adrienne L. Contasti

September 2011

Requests for permission to copy or make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Biology

University of Saskatchewan

Saskatoon, Saskatchewan S7N 5E2

ABSTRACT

Population-level dynamics are affected by temporal variation in individual vital rates of survival and reproduction, which are in turn influenced by habitat-specific processes. Variation in habitat quality within a population's range can drive movement of individuals between different areas, and so there may be a relationship between variation in vital rates and spatial heterogeneity in population growth (λ). I investigated this relationship for the feral horses (*Equus ferus caballus*) of Sable Island, Nova Scotia, Canada, from 2008−2010. The horses (n = 484 in September 2010) form a closed population that is free from human interference and predation. I analyzed annual population growth using age-structured projection matrix models parameterized with survival and fertility data collected from almost every female (98.7% of females). I found some evidence of temporal variation in growth during the two years I studied the population ($\lambda^{2008-2009}$ = 1.065, $\lambda^{2009-2010}$ = 1.117). Age structure appears to have converged to a stable age distribution, suggesting this growth rate has been sustained in the years leading up to the end of my study. Variation in vital rates of adult fertility and foal survival made the largest contribution to annual variation in population growth. Future growth is predicted to be most influenced by proportional changes in adult survival, which remained relatively unchanged between 2008 and 2010.

The population can be stratified into three spatially distinct subunits found across a west−east longitudinal gradient of water resources (access to permanent ponds vs. ephemeral water sources and holes dug in sand). I assessed the existence of source-sink dynamics to determine if individual movements between subunits could explain spatial heterogeneity in population growth. I found that spatial heterogeneity in growth appears to be most influenced by immigration and emigration events between subunits. Evidence suggests that current growth of the overall Sable Island horse population is made possible by individual emigration from more productive into less productive subunits; in particular, a source presented in the west of the island where permanent water ponds are located.

ACKNOWLEDGEMENTS

My research on Sable Island was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), the Canada Foundation for Innovation, and the University of Saskatchewan (through grants to Dr. McLoughlin). I was supported by an NSERC Post Graduate Scholarship and a University of Saskatchewan Teaching Fellowship. In-kind and logistical support was provided by Maritime Air Charters Limited, the Bedford Institute of Oceanography (Fisheries and Oceans Canada), and the Sable Island Weather Station. GIS mapping from Allison Muise and David Colville, of the Applied Geomatics Research Group at Nova Scotia Community College, was integral for Chapter 3.

I thank my Supervisor, Dr. Philip McLoughlin, for providing me with the privilege of working on Sable Island. Phil, you always knew exactly what to say to calm my doubts regarding my work. I thank my Advisory Committee for time, consideration, and encouragement. Drs. Trent Bollinger, Gary Bortolotti, Bob Clark, and Karen Wiebe.

I thank my father for teaching me the importance of self reliance but the beauty of working together. I thank my mother for teaching me perseverance, courage, and compassion.

I thank those who provided assistance on Sable and the mainland: Emily Tissier, Kenton Lysak, and Adia Sovie. I thank my student colleagues at the University of Saskatchewan and the Department of Biology. Special thanks to my teacher, Dr. Jill Johnstone. To my distant and close friends. I wish everyday could be Thursday.

To my hero, my rival, my biggest fan.

Because of your support, your understanding, your lending hand.

You are my link to the past and my key to the future.

My brother, my friend.

For Dean

May our paths always lead back together.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

1.1 INTRODUCTION

Our ability to predict how a population will respond to changing environmental conditions (Sæther 1997, Clutton-Brock and Coulson 2002, Coulson et al. 2004), conservation strategies (Crouse, Crowder, and Caswell 1987, Morris and Doak 2002, Mayberry and Elle 2010), or management practices (Dixon et al. 1997, Neubert and Caswell 2000) relies heavily on understanding the basis of population growth. Population-level dynamics are affected by individual life histories of survival and reproduction, which are in turn influenced by habitat and ecological processes like environmental stochasticity, habitat quality, density dependence, competition, and predation (Coulson et al. 1997, Sæther 1997, Sanz 1998, Gaillard, Festa-Bianchet and Yoccoz 1998, Virgl and Messier 2000, McLoughlin et al. 2005, 2006). Many wild populations occupy areas that are spatially heterogeneous with respect to ecological and habitat variables. Members of the same population may thus exhibit area-specific variation in fitness, which may lead to spatial heterogeneity in population-level growth (Pulliam 1988, Pulliam, Dunning, and Lui 1992, McPeek and Kalisz 1993, Coulson et al. 1997).

1.1.2 The basis of population growth

Understanding the basis of population growth has been a longstanding concern in ecology. A central problem is determining how 'vital rates' of survival and reproduction translate into population growth when these rates are known to vary for different classes of individuals (e.g., by age and sex; McPeek and Kalisz 1993, Gaillard et al. 1998 and 2000, Coulson et al. 2005). For example, in many mammals, juvenile survival shows considerable temporal variation compared to adult survival, as young are more vulnerable to harsh weather conditions (Forchammer et al. 2001 for Soay sheep *Ovis aries*, Coltman et al. 1998, harbour seals *Phoca vitulina*), poor-quality resources (Monard et al. 1997 for feral horses), or density-dependence (Coulson et al. 1997 for red deer *Cervus elaphus*). In addition, survival and reproduction rates may vary for the same classes of individuals living in different areas (Pulliam 1988, Gaillard et al. 2010). For example, in small mammals, adult over-winter survival is lower for individuals living in poor-quality areas compared to those living in good-quality areas (see: Virgl and Messier 2000 for the effect of low water availability on muskrats *Ondatra zibethicus* L.; Kreuzer and Huntly 2004 for the effect of snow cover on American pikas *Ochotona princeps* L.).

Similarly, in ungulates, reproductive success is greater for prime-aged females in possession of high-quality home ranges compared to those with low-quality home ranges (Berger 1986 for feral horses, Guinness et al. 1978 for red deer).

For discretely growing populations, matrix population models (Leslie 1945, Lefkovitch 1965) facilitate our understanding of how structure in vital rates affects a population's finite rate of increase (λ). By assigning sensitivity and elasticity values to vital rates, matrix models rank, in relative terms, how future dynamics will be influenced by absolute (sensitivity) or proportional (elasticity) changes in rates (McPeek and Kalisz 1993, Caswell 1997, Caswell 2001). For example, a higher ranked elasticity value for adult vs. juvenile survival in a mammal (e.g., Brault and Caswell 1997 for orca *Orcinus orca*; Galliard et al. 2000 for a review of ungulates) or bird (see Sæther and Bakke 2000 for a review) population suggests that a proportional change in the former would have a stronger influence on population trajectory than the latter. In this case, it may be tempting to conclude that adult female survival makes the greatest contribution to population change; however, recent research on age-structured populations has shown that changes in λ may not always be due to variation in the vital rate which ranks highest in elasticity analysis (Horvitz et al. 1997, Gaillard et al. 1998, Albon et al. 2000). The key to understanding temporal changes in λ is consideration of how different rates compare from one time interval to another, or from one habitat to another.

1.1.3 Source-sink dynamics and spatial heterogeneity in population growth

For mobile individuals, Pulliam (1988) originally proposed a source-sink dynamic model to explain the population-level consequence of active dispersal between areas of different quality. In his model, Pulliam (1988) defined good-quality 'sources' and poor-quality 'sinks' as having contrasting (i.e., heterogeneous) rates of population growth, and suggested that immigration and emigration between these areas may maintain total population size in an evolutionarily stable process. Traditionally, researchers have used Pulliam's (1988) definitions to identify source areas by $\lambda > 1$ (i.e., positive growth), high rates of survival and reproduction, a large and constant population size, and as being net exporters of individuals. Sink areas are identified by $\lambda < 1$ (i.e., negative growth), reproduction which does not balance mortality, a low and variable population size, and as being net importers of individuals (Thomas and Kunin 1999, Howe et al. 1991). Over ecological time, heterogeneity in population growth between sources and sinks leads to a

surplus of individuals in source areas. As local density in source areas increases, decreased mating opportunities and resources are predicted to be associated with increased emigration to low density sinks (Pulliam 1988). Such movement patterns lead to more variable changes in sink population size compared to more steady changes in source population size (Pulliam 1988, Howe et al. 1991).

Since Pulliam's (1988) work, movements of individuals between different areas have been found to influence area-specific demography and total population size (Howe et al. 1991, Watkinson and Sutherland 1995, Thomas and Kunin 1999, Hanski 2001, Zachariah Peery, Becker, and Beissinger 2006). For example, emigration from areas where survival is high to areas where survival is low can offset losses associated with poor-quality resources (e.g., Foppen et al. 2000: reed warblers *Acrocephalus scirpaceus*, Virgl and Messier 2000: muskrat), environmental catastrophes (e.g., Johnson 2004: flood related mortality in rolled-leaf beetles *Cephaloleia fenestrata*, C.), and predation (e.g., Cronin, Haynes, and Dillemuth 2004: effect of spiders on planthopper *Prokelisia crocea* mortality and dynamics). When losses in areas where survival is low (i.e., sinks) are offset by immigration, total population size, and thus λ, appears to be maintained in a stable process (Pulliam 1988). Source-sink dynamics for many populations of insects, birds, and small mammals suggest that the population-level consequence of active dispersal between different areas agrees well with Pulliam's model; however, studies of source-sink dynamics are rare for large-bodied mammals. In addition, few studies have determined the realized influence of active dispersal on area-specific demography (Watkinson and Sutherland 1995, Virgl and Messier 2000, Zachariah Peery et al. 2006, Naranjo and Bodmer 2007, Robinson et al. 2008), leaving both the cause of spatial heterogeneity in population growth and the true population-level consequence of internal source-sink dynamics unanswered. Indeed, such questions can only be addressed by following movements of marked individuals, particularly in a closed system, where all possible dispersers and non-dispersers for each area are known.

1.1.4 Structure in vital rates, internal source-sink dynamics, and the Sable Island feral horses

Long-term studies of ungulate populations have indicated that variation in vital rates is the most influential factor leading to temporal variation in population growth (e.g., Gaillard et al. 1998 and 2000 for review), and that this variation may be linked to area-specific survival and reproduction (Coulson et al. 1997, Gaillard et al. 2010). For example, temporal variation in

juvenile survival greatly influences red deer population growth (Coulson et al. 2004, 2005, and 2006), and varies between areas of different resource quality (Guinness et al. 1978) and local density (Coulson et al. 1997). Therefore, there may be a relationship between individual vital rate variation and source-sink dynamics, which may lead to spatial heterogeneity in population growth (McPeek and Kalisz 1993, Amarasekare 1994, Kreuzer and Huntley 2003, Pelletier et al. 2007). Understanding the population-level effect of variation in survival and reproduction (Sæther and Bakke 2000, Coulson, Gaillard, and Festa-Bianchet 2005, Pelletier et al. 2007), fitness-area relationships (McLoughlin et al. 2006, 2007, 2008, Gaillard et al. 2010), and active dispersal between different areas (Virgl and Messier 2000, Zachariah Peery et al. 2006) is essential for determining how individual dynamics relate to population-level dynamics.

Here I focus on quantifying the basis of discrete population growth for the feral horses on Sable Island, Nova Scotia, Canada, observed between 2008 and 2010. This system presents a unique opportunity to study dynamics of a large (n = 484 in September 2010), closed population in which life history events for each population member can be monitored. Although the Sable Island system has considerable potential for understanding the link between individual and population-level dynamics, the horses have not been studied in scientific detail since 1975 (Welsh 1975). Thus, my analyses are limited to two animal years (1 August−31 July) of survival and reproductive data, and explain population dynamics only in relation to current environmental conditions. However, by analyzing annual population dynamics separately, and by using survival and reproductive rates for each member of the population, I expected to be able to determine how observed variation in vital rates contributes to yearly variation in λ.

Following investigation of the underlying factors driving current population growth, I assess the existence of source-sink dynamics on Sable Island by identifying source subunits which may supplement growth in less productive areas of the island. Because the population is a closed system, I was able to follow the fates of each population member and accurately record the age and number of individuals that moved between ecologically distinct areas. This allowed me to determine the realized influence of immigration and emigration on area-specific demography, which allowed me to assess spatial heterogeneity in population growth. Therefore, my approach is a first step toward understanding the influence of area-specific demography on population-level growth, and may uncover the actual demographic effect of internal source-sink dynamics.

1.2 INTRODUCTION TO SABLE ISLAND AND ITS FERAL HORSES

When I began this study, I was interested in both ecological and evolutionary dynamics, and so I used a total island census regime and monitored almost every individual in the population. Coincidentally, I collected passive observational data regarding general survival, age- and sex-structure, sociality, mating, and spatial distribution for the population. The following sections and Appendix A provide current (2008−2010) information for the study system.

1.2.1 Study Site

All data were collected on Sable Island, Nova Scotia, Canada (Figure 1.2.1) between May and September 2008−2010. Sable Island (43°55′N; 60°00′W) is an approximately 3,000 ha crescent shaped sand bar located 285 km east of Halifax, Nova Scotia, Canada. Sable Island is nearly 50 km long and 1.2 km at its widest (AGRG 2011).

The island's climate is temperate oceanic. Winter temperatures ranged from -11.4°C to 15.8°C during the first year of my study (November 2008−March 2009) and from -10.8°C to 15.6°C during the second year of my study (November 2009−March 2010; Environment Canada 2011). Maximum summer temperatures reached 24.1°C in August 2009 and 22.3°C in July 2010 (Environment Canada 2011). These conditions were comparable to normal winter temperatures ranging from -10°C to 5°C, and maximum summer temperatures of 25° C (Environment Canada 2011). Precipitation falls predominantly as rain: yearly precipitation averages 124 cm, snow accounts for only 9% of the total (Environment Canada 2011).

Sable Island's plant communities are limited mostly to grasses covering approximately 40% of the total area (de Villiers & Hirtle 2004). Vegetated areas are restricted between the north and south beaches; salt-resistant, colonizing plants (e.g., sandworts, *Honckenya peploides*) tend to be located close to the beach (de Villiers & Hirtle 2004). Catling et al. (1984) details the flora present on Sable Island. Inland areas tend to support a higher diversity of marram-forb grasslands (*Ammophila breviligulata, Lathyrus maritimus, Achillea lanulosa, Solidago sempervirens*). Sparse grasslands of marram (*Ammophila breviligulata*) and marram-fescue (*Anaphalis margaritacea, Festuca rubra, Fragaria virginiana, Myrica pensulvanica, Rosa virginiana*) tend to dominate the vegetated area. Shrub heath (*Empetrum nigrum, Juniperus*

communis, *Myrica pensylvinica*, *Rosa virginiana*, *Vaccinium angustifolum*) and cranberry heath (*Vaccinium macrocarpon*) flourish in the middle of the island, along with other species of lichens and bryophytes. Quality and palatability of vegetation on Sable Island as forage for horses is unknown.

Confined to specific areas of the island and covering only 21.8 ha (0.73%), are several permanent water ponds (pH 5.0−5.7) of varying depth and water quality (Catling et al. 1984, AGRG 2011), which are used by horses for. Many of the shallow ponds in the eastern areas dry up in the summer; however, by digging into the sand, horses in the east can access the high water table (de Villiers & Hirtle 2004, Lucas et al. 2009). I directly observed horses excavating water holes inland at dried ponds and on the beach close to inland vegetation.

The fauna on Sable Island is limited to a few species of insects, arthropods, molluscs, birds, and mammals (National Museum of Natural Sciences Canada 1970). The only mammals aside from the horses are populations of breeding harbour and grey seals (*Halichoerus grypus*). Although there may be some competition for space during the summer between horses and common terns *Sterna hirundo* (which have several colonies inland, personal observation), or during winter between horses and seals (which pup on the island), the horses do not experience interspecific competition or any risk of predation.

1.2.2 Study Species

Origins of the Sable Island horses are mysterious. Some historians suggest the horses were left on the island after brief colonization by French during the 1500s (Christie 1995), while others claim the horses were introduced by Reverend Le Mercier in or around 1739 (Patterson 1894; Armstrong 1981). The population has always been free-ranging and was last 'managed' by humans (i.e., introduction of breeding stock mares and stallions of several different breeds) in 1940 (Christie 1995; Plante et al.2007). Genetically isolated on the island since then, the population was also formally protected from human interference under the Canada Shipping Act in 1960 (de Villiers & Hirtle 2004). As a result of this protection, my sampling was limited to non-invasive techniques.

Historical records of population size fluctuate between 150 and 400 (Welsh 1975, Lucas et al. 2009). However, there are no detailed records of population size from 1975 to 2008.

Between 2008 and 2010, I observed a population increase from 390 to 484 horses counted after birth occurred during each year (i.e., post-birth pulse; Appendix A, Table A.1.3.1).

1.2.2.2 Survival

Survival rates for many ungulates vary between ages and seasons (see Gaillard et al. 2000 for review); variation is highest in juveniles and tends to be influenced by harsh weather (Berger 1986, Garrott et al. 2003). Harsh winter conditions are responsible for most mortality on Sable Island (Welsh 1975, Lucas et al. 2009).

Survival during the summer months of 2008, 2009, and 2010 was high for all ages (excluding foals). I observed one death of an adult female during the 2010 field season. Mortality of newborns is high during the first few weeks following parturition for many ungulates (e.g., McCort 1984 for feral horses; Sæther1997 for a review of moose *Alces ales*, elk *Cervus elaphus canadensis*, big horn sheep *Ovis aries*; Albon et al. 2000 for red deer). Due to timing of my field work, I could not document early mortality of foals, although, I did find one foal carcass in 2008, five in 2009, and three in 2010. Of all dead foals observed, five appeared to have died *in utero* or during parturition.

Most mortality occurred in my absence (which I considered winter survival), although winter survival was relatively high for all ages and sexes (Appendix A, Table A.1.3.2). During the first year, age specific winter survival for males ranged between 0.91 and 1.00, and was slightly higher than female survival (0.88 to 0.98). Conversely, during the second year, female winter survival ranged between 0.91 and 1.00 for all ages and was higher than male survival (0.86 to 0.93).

1.2.2.3 Population structure

I identified 554 individuals during my study. Age and sex ratio were similar to other populations of free-ranging feral horses (Salter and Huson 1982; Linklater et al. 2000). Average post-birth, summer sex ratio was 0.88 adult (≥4 years old) males per adult female; 1.33 young (2- and 3-year-olds) males per young female; 1.20 yearling (1-year-olds) males per yearling female; and 1.21 foal (0-year-olds) males per foal female (Appendix A, Table A.1.3.3).

1.2.2.4 Social structure

Sable Island horses exhibit a social system similar to other species of wild equids, characterized by persistent, non-territorial groupings (Salter and Hudson 1982, McCourt 1984, Moehlman 1998, Linklater 2000). I observed horses in one of four social groupings: family bands, mixed adolescent groups, bachelor groups, or as solitary individuals.

Family bands were composed of several mares, their pre-dispersing offspring, and as many as three stallions. Family band size ranged from 6.1 to 6.6 horses during the study period; minimum band size was two, while was 15 (Appendix A, Table A.1.3.4). Bands were predominately made up of adult and young females (maximum 5 and 4, average 1.8 and 1.1, respectively). The largest number of family bands observed was 70 during 2010; the largest number of bands that had more than one stallion was 19 during 2008 (Appendix A, Table A.1.3.5). Membership in family bands was relatively consistent, as reported for other populations of feral horses (Salter and Hudson 1982, Linklater 2000, Linklater et al. 2000).

Young males and females were observed in mixed adolescent social associations without offspring. Such associations have rarely been observed in other feral horse populations (see: Linklater 2000 for review), and have been described as attempts by bachelor males to form their own bands (Salter and Hudson 1982). Of the five mixed adolescent groups I observed, one association was stable between 2008 and 2009 and resulted in the production of a foal (2009) before the association ended in 2010.

Bachelor groups were composed of males varying in age from young (i.e., recently dispersed from natal band) to elderly (i.e., adult stallions that had lost their family band to a younger stallion; Berger 1986, Linklater 2000). Membership in bachelor groups was highly unstable. Males of other feral horse populations leave bachelor associations and challenge stallions of family bands for mating opportunities, or form their own family band (Welsh 1975, Boyd & Keiper 2005). I observed the takeover of two family bands by a bachelor male in 2010. However, formation of new family bands by bachelor males occurred mostly between seasons (Appendix A, Table A.1.3.5).

Solitary individuals are rarely observed in other feral populations which have been attributed to shifting membership between bands (McGreevy 2004). I observed solitary

individuals during each field season. These were most frequently young males who had recently dispersed from family bands and adult bachelor males.

1.2.2.5 Band membership changes

Membership changes occurred most frequently when offspring dispersed from family bands (i.e., natal dispersal), but also due to emigration and immigration between family bands by adult mares. The majority of band membership changes occurred between seasons, although I did observe natal dispersal by a young female during each field season and a young male in 2009 and 2010. Offspring dispersed as yearlings and young individuals; overall, I observed dispersal by 34 females and 26 males (Appendix A, Table A.1.3.6). Yearlings were observed dispersing most frequently for both sexes, on average, females dispersed farther than males. Consistent with natal dispersal in other populations (Berger 1986), females tended to disperse to family bands while males dispersed to bachelor groups.

Adult female band membership changes occurred most frequently between parturition periods. I observed a total of 40 band membership changes by adult females either in a group with pre-dispersing offspring (foal and yearlings of both sexes) or as solitary individuals. Distance travelled by adult females ranged from 0.2 to 16.6 km (Appendix A, Table A.1.3.7).

1.2.2.6. Mating system

Sable Island horses exhibit a female-defence, polygynous mating system similar to other populations of feral horses (Welsh 1975, Salter and Hudson 1982, Berger 1986, Linklater 2000). Stallions in family bands have higher access to mates than bachelor males (Feh 2005). Band stallions defend reproductive aged females from copulating with external males. However, copulations with non-dominant males and band-takeovers occur (Welsh 1975; Berger 1986, personal observation), complicating assignment of paternity. Males usually reach maturity and begin producing sperm at 3-years, but many do not sire offspring until age 5 (Welsh 1975; Davies Morel 2008). Size differences between reproductive males and other horses were apparent on Sable Island (Welsh 1975, personal observation), but in general there was no marked

sexual dimorphism between adult males and females. I was unable to verify paternity and do not consider parentage for males in my analyses.

There is no mating rut on Sable Island: copulations normally occur between band stallions and mares 1 to 10 days after parturition (post-partum oestrus), or during the next oestrus (17 to 23 days later), until conception occurs (Welsh 1975; Davies Morel 2008). I observed copulations between stallion males and females that had recently given birth and those that had not. With gestation lasting 330−336 days (Welsh 1875; Davies Morel 2008), females give birth at most once per year, with the highest number of births occurring between April and June (Welsh 1975), similar to other populations of free-ranging horses (Salter and Hudson 1982, McCort 1984).

Females reach maturity and can give birth at age 2, but many do not foal until 4- or 5-years-old (Welsh 1975, Cameron et al. 1999, Davies Morel 2008). All surviving foals from the 2009 and 2010 cohorts were produced by 3-year-olds and adult females. This means that 3-year-old mares would have been impregnated as 2-year-olds, and thus I consider 2-year-old females to be of reproductive age.

1.2.2.6 Band interactions and spacing behaviour

I was unable to collect sufficient GPS (Global Positioning System) locations to calculate home range size. Bands can have distinctive home ranges varying in size from 0.92−6.62 km^2 (Welsh 1975), where core areas are defined by access points for food and water (Salter and Hudson 1982, Berger 1986). Being non-territorial, home ranges of several bands often overlap, as for other horse populations, resulting in sharing of available resources (Welsh 1975, Salter and Hudson 1982, Linklater et al. 2000). I frequently observed family bands, mixed adolescent groups, and bachelor groups in close proximity, but mixing of individuals from different bands was almost never observed.

For other horse populations, distribution is known to change with seasonality in plant communities, shelter, and water availability (McCort 1984, Linklater 2000). Similar changes in distribution were observed on Sable Island (Welsh 1975). Home ranges of some bands contained permanent water ponds that were used daily. Horses in areas without permanent water

ponds accessed water by digging into the sand in areas close to the water table (Welsh 1975, personal observation).

1.2.3 Field methods and census design

I collected data on Sable Island, Nova Scotia, Canada, during the mid- to late-summer seasons of 2008 (12 August–9 September), 2009 (23 May–22 July), and 2010 (22 July–1 September). As horses have a birth-pulse reproduction schedule and almost all females give birth between April and August, my field seasons fell during that period in each year. I performed complete censuses of the island each field season to locate every individual. I conducted a total of 38 censuses during 2008, 49 in 2009, and 40 in 2010.

I drove to a predetermined sampling area on each census day (areas differed daily; Appendix A, Figure A.1.4.1 for sampling areas); all vehicle travel was restricted to the beach. I divided the island into eight different sampling areas based on landscape features and density of horses; walking censuses were completed within 5 hours, between 08:00 and 19:00, with the aid of a field assistant. I monitored individual horses based on unique face and body markings described in field notes and from digital photographs. This method that has been successful for monitoring individuals of wild and feral equids (See: Llyod & Rasa 1989 for Cape mountain zebra; Rutberg & Keiper 1993 for feral horses of Assateague Island; Saltz & Rubenstein 1995 for Asiatic wild ass *Equus hemionus*; Heitor, do Mar Oom, & Vicente 2006 for Sorraia horses *Equus caballus*). During each census, I recorded the identity and position of each horse observed using a handheld GPS and took digital photographs. I confirmed identities using a photo-identification database created in 2008 that catalogued all horses alive. All locations were accurate between 4 and 7 meters for each horse. As there are no trees on Sable Island, horses were easily located by climbing dunes and scanning the landscape with or without the aid of binoculars.

At the beginning of each field season, I conducted a detailed census of the entire island in which I located each individual to establish a total post-birth pulse population size. From total count data, I established births that were not recorded during the previous year (i.e., 2008 and 2009) and quantified deaths of individuals known to be alive the previous year. As Sable Island

is a closed system, all individuals known to be alive at the end of one year which I did not find the following year were assumed to be dead.

I was able to distinguish between late-born foals of the previous year's cohort (i.e., yearlings) and foals of the current year's cohort based on body size and coat type. Yearlings were larger in size than foals and had evidence of winter coats, as opposed to the birth coats of foals. All individuals first observed as yearlings were added to my database in the appropriate year's cohort.

1.2.3.1 Sex Determination

Sexing horses was relatively straightforward by direct observation of external genitalia (Cameron et al. 1999). Although possible immediately following birth, sexing newly born foals was sometimes difficult due to their small size and protection by mares. In situations where I was unable to sex a foal during a census, I took digital photographs, recorded appearance notes, and determined maternity information so that I could sex the foal at next observation.

1.2.3.2 Female condition scoring

I assigned each female ≥2-years-old a body condition score at each observation. Body condition scoring is reliably applied to various species and breeds of equids that enables ranking and comparison between individuals (Carroll & Huntingdon 1988). Condition is also known to influence reproductive success (Cameron et al. 1999, Cameron and Linklater 2007). The method estimates body condition from 0−5, based on visual observation of fat distribution in 11 places on the body (Carroll & Huntingdon 1988). Half scores are allowed in this system. A condition score of 0 is given to extremely emaciated individuals, while a score of 5 mean an individual was extremely obese.

1.2.3.3. Maternity Assessment

I assigned the mother of each foal based on direct observation. The mare-foal relationship is strongest shortly after birth; foals remain close to their mothers for the first four weeks

(Moehlman 1998, Ladewig, Søndergaard & Christensen 2005). Mares only nurse their own offspring (Welsh 1975; Feh 2005). I assigned maternity information for females observed nursing foals of the current year's cohort and yearlings of the previous year's cohort.

1.3 THESIS STRUCTURE

The remainder of my thesis is divided into three Chapters. In Chapter 2, I quantify and investigate the basis of current population growth for the Sable Island horses. In Chapter 3, I use annual movements of females between three spatially distinct subunits to uncover source-sink dynamics on Sable Island. I identified areas which produced more emigrants and areas which accept more immigrants to determine if spatial heterogeneity in population growth can explain current population growth (Chapter 2). In Chapter 4, I present final conclusions and provide recommendations for future research.

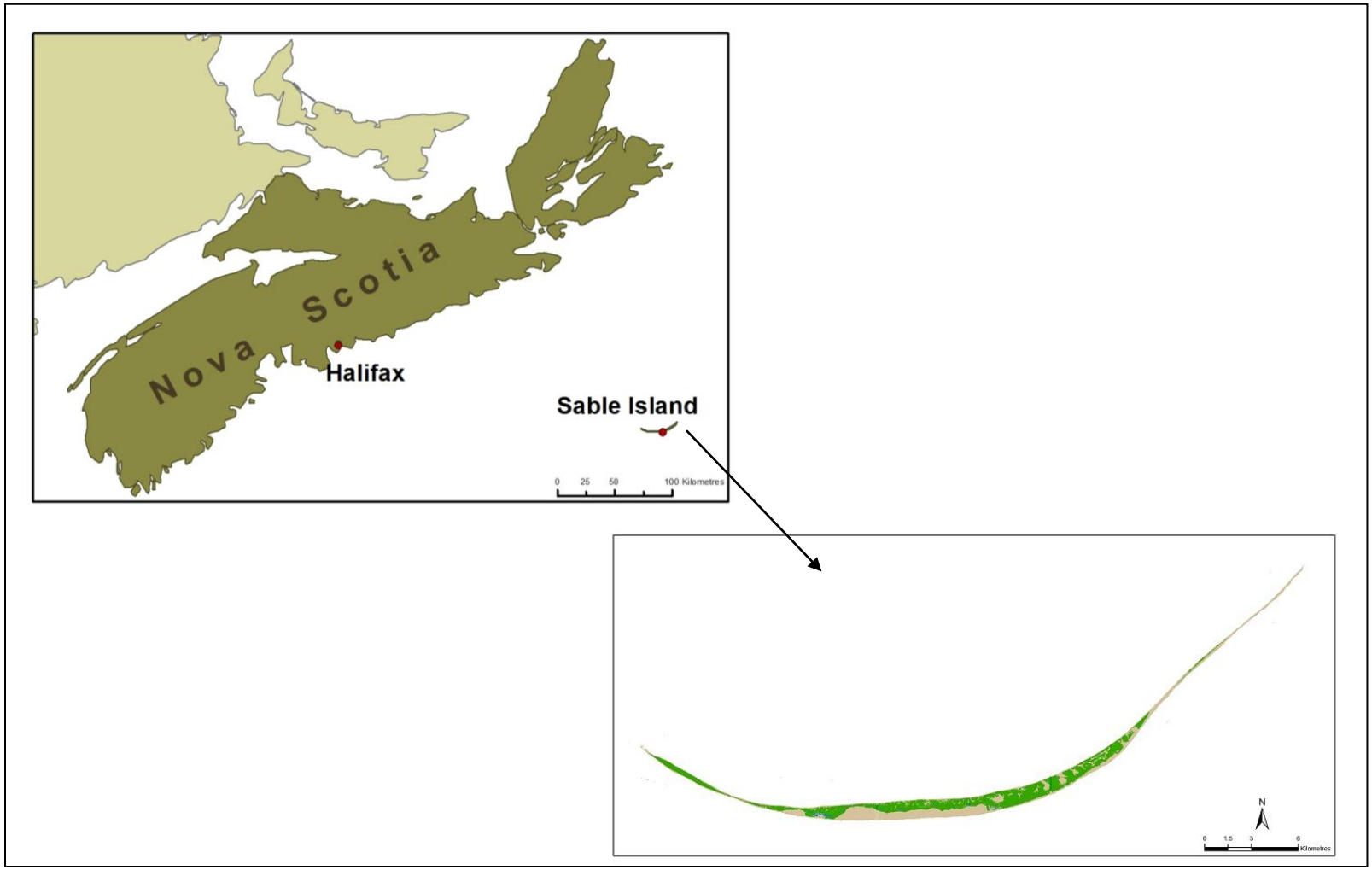

Figure 1.2.1. Sable Island, Nova Scotia, Canada (43°55′N; 60°00′W), located approximately 285 km east of Halifax, Nova Scotia. The island is a crescent shaped sand bar (approximately 3,000 ha in area) nearly 50 km long and 1.2 km at its widest. Map credit: AGRG 2011.

CHAPTER TWO: THE BASIS OF CURRENT POPULATION GROWTH OF THE SABLE ISLAND FERAL HORSES (*Equus ferus caballus*)

2.1 INTRODUCTION

Long-term studies of ungulate populations have shown that environmental stochasticity and density dependence have a strong influence on age-specific vital rates of survival and reproductive (Sæther 1997, Albon et al. 2000, Coulson et al. 2004), and that variation in these rates is the basis of temporal variation in population growth (λ; Gaillard et al. 1998 and 2000, Coulson et al. 2005). The overall influence of each rate on population growth is determined both by its magnitude of temporal variation and elasticity value. Across most ungulate populations, adult survival consistently ranks highest in elasticity value compared to all other age-specific rates (e.g., Garrott et al. 2003 for elk, Johnson et al. 2010 for Sierra Nevada big horn sheep *Ovis canadensis sierrae*), but tends to show the least variation compared to juvenile survival, which is more vulnerable to limiting factors (Albon et al. 2000, Gaillard et al. 1998 and 2000, Raithel et al. 2007). Elasticity values estimate the influence that a potential change in an age-specific vital rate has on λ; however, they do not measure realized contributions resulting from actual temporal variability in each vital rate. Hence, considering vital rate elasticity values without data on temporal variation may not identify true reasons for natural changes in population size (Horvitz, Schemske, and Caswell 1997, Coulson et al. 2005). To fully understand a population's dynamics requires knowledge about the underlying factors that cause vital rates to vary temporally, the relative influence of each vital rate on population growth (i.e., elasticity), and the actual magnitude of temporal variation in each vital rate.

Here, I am interested in quantifying and understanding the basis of population growth for of the feral horses on Sable Island observed between 2008 and 2010. The horses (see Chapter 1.2.2) present a unique opportunity to study dynamics of a population free from predation pressure and human management (e.g., round-ups and culling), where population size is controlled wholly by births and deaths. My objectives were to: (1) estimate the finite rate of population increase (λ) from survival and fertility rates observed during each year; (2) predict population age-structure if λ were to remain constant by calculating the stable age distribution, and then compare predicted vs. current age-structure; (3) determine which age class has the greatest potential to contribute to future population size by calculating reproductive values; (4) determine the proportional influence that changes in each rate will have on future λ using an elasticity analysis (prospective analysis); (5) assess the magnitude of temporal variation in λ by comparing results for objectives 1 through 4; and (6) determine the overall contribution that

actual variation in vital rates made to the observed difference in λ using a retrospective analysis. Specifically, I was interested in determining the basis of current population dynamics observed on Sable Island.

Due to limited data, I was unable to determine the underlying factors that cause vital rates to vary through time; my analyses do not consider the effects of environmental stochasticity or density dependence. However, I expected that demographic stochasticity (i.e., random variation between individuals) would cause all vital rates to vary temporally between years (Kalisz and McPeek 1993, McPeek and Kalisz 1993, Albon et al. 2000); thus, λ should also vary annually. By analyzing population dynamics for the two years separately and calculating vital rates from individually monitored horses, I measured how actual variation in vital rates contributed to the difference in observed λ. I predicted that changes in adult survival would have the largest proportional effect on future λ compared to all other vital rates, similar to other ungulate populations (Galliard et al. 2000, Garrott et al. 2003, Johnson et al. 2010). However, considering the state of current population growth (see Chapter 1.2.2.1), I expected that adult survival would not vary compared to juvenile (foal and yearling) survival (Gaillard et al. 1998, Albon et al. 2000, Harris, Kauffman, and Mills 2008). If adult survival has the largest proportional effect (i.e., elasticity value) on future λ, but remains relatively constant between years, I predict that any observable variation in λ will be a result of variation in vital rates with lower proportional effects on λ.

2.2 METHODS

2.2.1 Study species

I analyzed data from female horses on Sable Island (see Chapter 1.2.1 for a detailed description). Females reach maturity and can give birth at the age of 2, but most do not foal until age 4 or 5 (Welsh 1975; Davies Morel 2008). However, as reproduction is possible for 2-year-olds (e.g., Berger 1986 for feral horses), I considered females ≥2-years-old to be of reproductive age. Females were aged based on visual observations made each year; individual ages were verified and amended to ensure no female was assigned to the same age class in consecutive years (excluding females in age class adult). Foals (age 0), yearlings (age 1), and adults (≥4 years) were distinct from 'young' individuals, which I defined to be between 2 and 3 years of age

(Figure 2.2.1). Therefore, it is possible that the 2008 age-distribution contained errors for counts of 2- and 3-year-olds. Reproductive senescence has been observed in other species of ungulates (see Gaillard et al. 2000 for review). However, I was unable to distinguish between prime and reproductively senescent adult females, and therefore considered all females ≥4-years-old as adults.

2.2.2 Field methods

Data were collected during the summers of 2008 (12 August–9 September), 2009 (23 May–22 July), and 2010 (22 July–1 September). I performed complete censuses of the island during each field season (see Chapter 1.2.3 for a detailed description).

I conducted daily walking censuses with the aid of a field assistant within a set sampling area of the island (Appendix A, Figure A.1.4) and recorded the identity, position, field age, and foaling events for each female observed. I confirmed identities using a photo-identification database, which catalogued all horses alive and born into the population over the study period.

I gathered a minimum count for each age class during annual censuses. However, because I monitored individuals and performed complete and repeated island censuses during each year, my count data were representative of near-complete population numbers. Of all females alive during the study, I knew 98.7% (236 of 239) individually. I removed three females from analyses that I could not positively identify. Missing horses was highly unlikely as Sable Island is devoid of trees and my methods, which included walking surveys along both the north and south beaches and scans from the highest elevations in a sampling area, were comprehensive. My island-wide count of horses for 2009 was confirmed with 99% accuracy using aerial photography (D. Bowen, Bedford Institute of Oceanography, Fisheries and Oceans Canada).

2.2.3 Analysis

I applied a female-based, age-structured, projection matrix analysis to two animal years (1 August−31 July) of survival and fertility (where fertility is a proxy for reproduction; see 2.2.3.1) data to describe current population dynamics (Caswell 1997, Caswell 2001). I added a level of certainty to analyses using bootstrap resampling based on individual survival and fertility events

(Kalisz and McPeek 1993, Caswell 2001, Picard et al. 2009). A prospective matrix analysis (elasticity analysis) was used to predict how future λ would respond to proportional changes in each vital rate (Caswell 1997, Caswell 2001), and a retrospective matrix analysis was used to determine the realized influence of vital rates on annual differences in λ (Caswell 1996, Horvitz et al. 1997, Albon et al. 2000, Coulson et al. 2005).

I used two age class-structured matrix models (Leslie 1945) to estimate annual demographic parameters (2008–2009 and 2009–2010); I compared 95% bootstrap confidence intervals to identify variation between years. Models used in analyses were linear, time invariant population projection matrix models (McPeek and Kalisz 1993, Caswell 1997, Caswell 2001) which described dynamics of the female portion of the population only. For large herbivores with a polygynous mating system, the number of males required to ensure fertilization is far less than the total number of females (Mysterud, Coulson, and Stenseth 2002). As I assumed that both male and female schedules of survival and reproduction are fixed in each year, the value of λ appropriate to the male portion will be the same as λ for the female portion of the population (Caughley 1977: 180). The data I used to construct models were collected during post-birth seasons (end-July to end-August). Because parturition occurs once a year between April and August for almost all females (Welsh 1975; personal observation), I used a birth-pulse projection and a post-birth pulse census procedure to estimate survival and fertility probabilities (Caswell 2001, Morris and Doak 2002, Iverson and Esler 2010).

The general structure of each model described the relationship between $\boldsymbol{N}_{(t+1)}$ and $\boldsymbol{N}_{(t)}$ for each annual projection interval as:

$$\boldsymbol{N}_{(t+1)} = \mathbf{A}^{t \text{ to } t+1}\boldsymbol{N}_{(t)}$$

where $\boldsymbol{N}_{(t+1)}$ is a vector representing age-structure at the end of each projection interval, $\boldsymbol{N}_{(t)}$ is a vector representing age-structure at the beginning of each projection interval, and $\mathbf{A}^{t \text{ to } t+1}$ is the projection matrix model for each year. Because $\mathbf{A}^{t \text{ to } t+1}$ is a constant matrix which assumes elements do not vary over time (Kalisz and McPeek 1993, Caswell 1997), I constructed a separate matrix for each year, $\mathbf{A}^{2008–2009}$ and $\mathbf{A}^{2009–2010}$ (Figure 2.2.2), and parameterized non-zero elements using survival and fertility rates estimated from data for females in each age class during a given year.

2.2.3.1 Vital rates

For each year *t* to *t* + 1, I created a census age-class-fate dataset which contained the following information for each female: (1) age class at *t*; (2) fate at *t* + 1, where fate was either survival (i.e., transition to next age-class) or death; and (3) an individual fertility value at *t* + 1. Age class survival and fertility rates were calculated for each year.

Survival

I distinguished between active season survival (i.e., 'field-season survival') and winter survival for yearlings, 2-year-olds, 3-year-olds, and adults, but because I considered the birth pulse and post-birth pulse to be the active season, I could not account for foal deaths which occurred in the first few weeks following parturition. Therefore, I defined foal survival as the number of surviving individuals at *t* + 1 which were alive at *t*. Foal survival was considered a measure of recruitment (Gaillard et al. 1998).

I defined 'field-season survival' as survival over the period of summer censuses. 'Field-season mortality' was defined as failing to re-sight an individual known to be alive at the beginning of my field season and by observation of carcasses that could be positively identified. If an individual was not re-sighted after two complete island censuses (approximately 8–9 days per island census), I considered that individual to have died.

I defined 'winter survival' to have occurred over the winter, i.e., between post-birth pulse seasons, for each year. As Sable Island is a closed system and disappearance of known individuals cannot be attributed to emigration, I assumed winter mortality occurred for individuals not observed in consecutive seasons. I used winter survival in analyses because it included foals in addition to all other age classes. For simplicity, hereafter I refer to winter survival as 'survival'. I estimated age class survival rates from each source dataset as the ratio of individuals alive at *t* successfully re-identified at *t* + 1 (i.e., fate other than dead) to individuals alive at *t*. I used log-linear models to test whether the five age classes differed in survival between years (Caswell 2001, Mayberry and Elle 2010) and employed an alpha value of 0.05 for all statistical tests.

Fertility

I used individual fertility values as a proxy for reproduction. I defined fertility as the number of surviving foals a female of age-class *i* produced by post-birth pulse censuses (*t* + 1) for each year (Caswell 2001, Morris and Doak 2002). Fertility data were recorded for females observed with

suckling offspring (Welsh 1975; Feh 2005); hence, fertility rates represented annual reproductive performance of 3-year-old and adult females. I considered reproductive performance as the production of a foal which survived to the end of post-birth pulse censuses at $t + 1$ (Albon et al. 2000).

Due to timing of my censuses, yearly birth counts only considered foals which survived the early period of their first summer. In ungulates, offspring mortality usually occurs immediately following parturition rather than in late summer or winter seasons (Welsh 1975, Sæther 1997, Garrott et al. 2003). It is possible that yearly birth rates were greater than those I counted during censuses because I could not account for early deaths. Therefore, my fertility rates are approximations of the true underling fertility distribution.

All females observed with a foal during census at $t + 1$ were given an individual fertility value. Fertility values equalled a female's age class probability of surviving the year from t to t +1, times the number of yearlings she is expected to contribute to the next year's census at t (Caswell 2001, Morris and Doak 2002, Iverson and Esler 2010). Because twinning is very rare in horses (I did not observe any), the maximum number of yearlings a female was ever expected to contribute to the next year, given she produced a foal that survived to $t + 1$, was one. Females not observed with a foal were given fertility values of zero. I added individual fertility values to the corresponding year's census age-class-fate dataset and calculated age class fertility rates as an average of individual fertility values. Using this method, I was unable to assign individual fertility values to females who were observed with a foal during the 2008 census because survival probabilities for the 2007−2008 year were unknown. I used log-linear models to test whether 3-year-old and adult females differed in fertility between years (Caswell 2001, Mayberry and Elle 2010). I used the R package MASS (Venables and Ripley 2002, R Development Core Team 2010) to perform log-linear analyses.

2.2.3.2 Matrix projection

I used the R package popbio (Stubben and Milligan 2007) to project the future state of the population based on conditions observed during each year. A deterministic projection estimated annual λ (dominant eigenvalue), stable age distribution (w, right eigenvector), and age class reproductive values (v, left eigenvector) for each matrix model.

I estimated the magnitude of λ for each matrix projection to determine the rate at which the population was growing during each year. A λ value >1 indicates population expansion, whereas a λ value <1 indicates population decrease; λ = 1 indicates stability (Caswell 2001).

The stable age distribution predicts future proportion of females in each age class if the population were to continue to grow at λ (Caswell 1997, Caswell 2001). I compared census-observed 2009 and 2010 age class proportions to stable age distribution for 2008−2009 and 2009−2010, respectively, using a chi-square test to determine if observed distributions were significantly different from predicted (Johnson et al. 2010). I used the R base package (R Development Core Team 2010) to calculate chi-square tests.

Reproductive values indicate the potential for each age class to contribute to future population size (McPeek and Kalisz 1993, Caswell 1997). For each year, reproductive values were rescaled to give foals a value of 1, allowing comparison between age classes (Caswell 2001).

I identified the most influential vital rates on population growth using a prospective (elasticity) matrix analysis (McPeek and Kalisz 1993, Caswell 1997, Caswell 2001). Elasticity values were assigned to each vital rate to quantify the change in λ expected from a proportional increase or decrease of that rate. For each year, vital rate elasticity values sum to 1 and are directly comparable. As the magnitude of elasticity values indicates how sensitive λ is to a specific vital rate, I considered those rates with the highest elasticity values to have the largest influence on future λ.

I used a retrospective matrix analysis (Brault and Caswell 1993, Caswell 1996, Horvitz et al. 1997, Coulson et al. 2005) to account for population-level effects that variation in survival and fertility rates had on λ. This method considers both elasticity values and actual temporal variation in vital rates, thus it is an appropriate method to estimate which rates are most strongly associated with temporal variation in λ (Caswell 1996, Coulson et al. 2005).

Retrospective methods involve comparison of matrix elements for the first and second year ($\mathbf{A}^{2009–2010}$ vs. $\mathbf{A}^{2008–2009}$). I used $\mathbf{A}^{2009–2010}$ as the reference matrix and calculated a matrix of differences between elements (i.e., age class vital rates) of $\mathbf{A}^{2009–2010}$ and $\mathbf{A}^{2008–2009}$. I created a mean matrix from elements of $\mathbf{A}^{2009–2010}$ and $\mathbf{A}^{2008–2009}$, and then used the mean matrix to calculate a matrix of sensitivities. A matrix of contributions, **C**, was created by multiplying the matrix of differences by the matrix of sensitivities. Contributions made by each rate are

presented as a graphical comparison. The elements in **C** summed to an approximation of the observed difference in λ between the two years (Caswell 1996), and indicated which rates made positive and negative contributions to $\lambda^{2009–2010}$. A positive contribution to $\lambda^{2009–2010}$ was made by a vital rate if it experienced an increase during the second year compared to the first. The highest contribution values indicated which vital rates were most strongly associated with temporal variation in λ between the two years.

Bootstrapping

Although survival and fertility data were collected from a near-complete census of the population and contained minimal sampling variance, my data are subject to process variance caused by demographic stochasticity, or genetic differences, inherent in natural populations (McPeek and Kalisz 1993, Caswell 2001). Because vital rates were subject to a small amount of uncertainty, demographic parameters estimated from a matrix model were also subject to uncertainty (Picard et al. 2009). I used a bootstrap method to describe the true, unknown distribution of yearly vital rates with an empirical distribution created by resampling individual histories (Kalisz and McPeek 1993, Manly 1998). A level of certainty was added by generating mean and 95% confidence intervals (CIs, percentile method) for each parameter (Caswell 2001). Bootstrap methods were appropriate because survival and reproduction data were collected from monitoring the same set of known females (Stubben and Milligan 2007, Picard et al. 2009).

I used census age-class-fate datasets, described in 2.2.3.1, as source datasets for bootstrapping, which was applied to each source dataset separately. A bootstrap data set was created from the source dataset by randomly drawing a number of individuals, with replacement, equal to the number of individuals in the source dataset. I calculated age class survival and fertility rates using individuals of the bootstrap dataset, and parameterized one matrix model using those rates (as described above in 2.2.3.1 and 2.2.3, respectively). I used the bootstrap matrix model to estimate demographic parameters: λ, stable age distribution, reproductive values, and elasticity values. I repeated this process 1000 times (Caswell 2001, Stubben and Milligan 2007, Picard et al. 2009) to generate mean and 95% CI estimates for each vital rate and demographic parameter.

I compared bootstrap estimated vital rates to census-calculated vital rates, using a chi-square test, to determine how well bootstrapped estimates fit with census data. For each year, I performed a deterministic projection of census-calculated vital rates and compared the results to

mean values predicted from bootstrap methods. I used 95% CIs to compare results from each matrix projection to determine the extent of variation in demographic parameters.

2.3 RESULTS

2.3.1 Census-calculated and bootstrap estimated vital rates

While field-season survival was high for yearlings, 2-year-olds, 3-year-olds, and adults, I did find carcasses each which could be neither identified nor sexed. Carcasses were in late stages of decomposition, suggesting that death had occurred prior to my arrival. Although I did not measure field-season survival for foals, I found one foal carcass in 2008 field season, five in 2009, and three in 2010. Four of the dead foals appeared to have died in utero or during parturition.

Annual census-calculated vital rates were not significantly different from mean vital rates estimated from 1000 bootstrap-generated datasets (Appendix B,Table B.2.3.1; 2008–2009: $\chi^2 <$ 0.0001, df = 6, $P > 0.999$; 2009–2010: $\chi^2 = 0.0002$, df = 6, $P > 0.999$). Log-linear models indicated that survival rates were not significantly different for females in different age classes during both years ($G^2 = 6.874$, df = 4, $P = 0.143$). Variation in vital rates between years was small (Table 2.3.1). For example, compared to 2008−2009, variation in 2009–2010 survival was greatest for foals ($2.862e^{-3}$), 2-year-olds ($1.156e^{-3}$), and yearlings ($1.320e^{-4}$), but relatively minimal for adults ($2.030e^{-5}$) and 3-year-olds ($2.500e^{-7}$). Log-linear models indicated that fertility rates were not equal between 3-year-olds and adults during either year, which was largely due to the influence of age class on fertility ($G^2 = 6.60^{-5}$, df = 1, $P = 1.85^{-5}$). Fertility was more variable compared to survival (Table 2.3.1). Fertility was greater for both 3-year-olds and adults during the second year. Three-year-old fertility was slightly higher than adult fertility in both years. Overall, survival rates were much higher than fertility rates. There was little variation between deterministic estimates and those calculated using bootstrapping (Appendix B, Tables B.2.3.2, B.2.3.3, B.2.3.4, and B.2.3.5).

2.3.2 Population growth rate

The total number of females increased during both years of my study. The population grew from 190 to 207 females during the first year ($\lambda^{2008–2009}$ = 1.065; 95% CI = 1.008–1.123), and increased from 207 to 237 females during the second year ($\lambda^{2009–2010}$ = 1.117; 95% CI = 1.061–1.170). Population growth during the second year was more rapid compared to the first, although 95% CIs overlapped.

2.3.3 Stable age distribution

If the female portion of the population continues to grow geometrically at a rate equal to calculated λ, population age-structure will eventually converge to the predicted stable age distribution (Table 2.3.2, Figure 2.3.1). Age structure is predicted to be dominated by adults. Census observed age structures from 2009 and 2010 were not significantly different from predicted stable age distributions (Table 2.3.2; 2009 vs. 2008–2009: χ^2 = 0.046, df = 4, *P* = 0.997; 2010 vs. 2009–2010: χ^2 = 0.013, df = 4, *P* = 0.999).

2.3.4 Reproductive values

Females in the 3-year-old age class had the greatest potential to contribute to future population size (Table 2.3.3), followed by adults, 2-year-olds, yearlings, and foals. During year 2, reproductive values for 3-year-olds and adults were slightly greater than year 1, compared to increases for all other age classes.

2.3.5 Prospective (elasticity) analysis

Future λ was predicted to be most affected by proportional changes in adult survival relative to all other vital rates (Figure 2.3.2). After the influence of adult survival, elasticity values indicated that future λ was best predicted to be equally affected by changes in foal, yearling, 2- and 3-year-old survival, and adult fertility; changes in 3-year-old fertility was predicted to have the smallest effect on future λ (Table 2.3.4).

2.3.6 Retrospective analysis

Mean estimates indicated the population was growing at a faster rate during year 2 ($\lambda^{2009–2010}$ = 1.117 vs. $\lambda^{2008–2009}$ = 1.065). My retrospective analysis indicated that the slightly greater λ during year 2 was influenced most by changes in adult fertility and foal survival (Figure 2.3.3).

Visual comparison of transition matrices $\mathbf{A}^{2008–2009}$ and $\mathbf{A}^{2009–2010}$ (Figure 2.2.2) indicated that almost all vital rates increased in year 2. Foal, yearling, and adult survival, and 3-year-old and adult fertility made positive contributions to $\lambda^{2009–2010}$ (Figure 2.3.4). Adult fertility and foal survival were most the variable vital rates (Table 2.3.1), and increases in these vital rates during the second year made the largest positive contribution to $\lambda^{2009–2010}$ (adult fertility = 0.034, foal survival = 0.013). Two- and 3-year-old survival had decreased in year 2, and these were the only rates that had a negative effect on $\lambda^{2009–2010}$. Negative contributions were relatively small compared to the positive values for all other vital rates. Elements of **C** summed to 0.053, which is an accurate approximation of the observed difference in λ between years ($\lambda^{2009–2010} – \lambda^{2008–2009}$ = 0.052). Adult survival, which had the greatest elasticity value (Table 2.3.4, Figure 2.3.2), remained relatively constant compared to changes in adult fertility and foal survival (Table 2.3.1).

2.4 DISCUSSION

I studied the Sable Island feral horses during a period of population expansion. Projection matrices indicated an increasing population trend during both years, which is consistent with increases in male and female census counts (390 to 484 horses) between 2008 and 2010. Although 95% CIs indicated there was no statistical evidence of temporal variation in λ, mean estimates indicated that growth was more rapid during year 2. As mean estimates were no different from deterministic projections using census-calculated survival and fertility rates, I considered population growth to be more rapid during year 2. I attributed this trend to increased adult fertility and foal survival during the second year. Adult survival, which was predicted to have the most influence on future λ, remained relatively constant and thus made little contribution to the faster growth rate during the second year.

Demographic studies often consider average vital rates calculated from decades of mark recapture or telemetry data (see: Gaillard et al. 1998, Pease and Mattson 1999, Garrott et al.

2003, Raithel et al. 2007), which are subject to both sampling and process variance; the effect of temporal variation in each vital rate on λ is then investigated in subsequent analyses (e.g., Brault and Caswell 1993, Sæther and Bakke 2000). One drawback of this approach is the inability to account for individual fertility values. Rather, many researchers rely on ratios of offspring to females as an estimate of fertility (e.g., Raithel et al. 2007, Johnson et al. 2010), which can be misleading (Bonenfant et al. 2005, Harris, Kauffman, and Mills 2008). Gaillard et al. (2000) reviewed demographic patterns of large-bodied herbivores and found that the most rigorous studies lasted at least three years and accounted for age-specific survival and reproduction by individuals. My conclusions come from data for individually recognizable female, but limited to two years. I believe that the reliability of my vital rate estimates is high because I conducted a near-complete (98.7% of all females) census. By analyzing population dynamics for each year separately, I accounted for temporal variation in vital rates with almost no sampling variance. My approach was similar to Coulson et al.'s (2004), who constructed annual projection matrices for a 30-year period to assess the impact that variation in vital rates had on changes in population size of red deer following release from culling.

The predictive power of my matrix models must be taken sceptically because projection methods estimate dynamics assuming that rates do not vary over time (McPeek and Kalisz 1993, Caswell 2001). I tested how temporal changes in vital rates influenced λ, but with no way of knowing long-term trends in vital rates. However, my purpose was not to predict future population dynamics; rather, my results were meant to explain the observed λ during my study, and to consider the relationship between the population and its environment during each year.

2.4.1 Current demographics

As expected, survival and fertility rates for females varied slightly between years. Survival was high during both years, consistent with other populations of feral horses on islands (Keiper and Houpt 1984). Adult females had lower and less variable fertility rates than 3-year-olds for both years, perhaps due to demographic stochasticity. Consistent with other populations of ungulates (e.g., Gaillard et al. 1998, 2000; Albon et al. 2000; Garrott et al. 2003), prime-aged female survival (here 3+ years old) was less variable between years compared to juvenile survival (foal, yearlings, and 2-year-olds) and reproduction.

Although I am confident in my survival rate estimates, adult fertility rates may be underestimated. Reproductive senescence has been reported ungulates (e.g., Albon et al. 2000 for red deer, Garrott et al. 2003 for elk) and it is possible, and perhaps likely, that very old females on Sable Island are beyond reproductive age. However, I was unable to distinguish between prime-aged and reproductively senescent females and grouped all females ≥4 years old as adults.

The short term nature of my study precluded consideration of the influence of environmental stochasticity and density dependence, both known to affect survival and fertility rates in many ungulates (Sæther 1997; Gaillard et al. 2000; Clutton-Brock and Coulson 2002 for red deer and Soay sheep). Instead, I only considered demographic stochasticity, or variation in genotypes between individuals (McPeek and Kalisz 1993), as a cause of vital rate variation. Because vital rates are affected by temporal changes in climate (Garrott et al. 2003), my results are only applicable to the relationship between λ and the specific environmental conditions during my study period. Density dependence is especially influential on offspring survival (Sæther 1997, Gaillard et al. 2000, Harris et al. 2008) and could have been a dominant factor. However, because density effects can take many years to become apparent (Peterson, Page and Dodge 1984, Couslon et al. 2004, Jacobson et al. 2004), I had no way of incorporating it into my models.

Census age structures were not different from the predicted stable age distribution. A population growing at a rate equal to λ will eventually converge to the stable age distribution regardless of initial conditions (McPeek and Kalisz 1993, Caswell 1997, Caswell 2001). Once a stable age distribution is reached, the proportion of individuals in each age class will increase in size at a rate equal to λ each year (Crouse et al. 1987, Brault and Caswell 1993). Thus, my results suggest that current λ has likely been sustained in this population for some time. However, because population numbers had not been monitored prior to 2008, I have no way of determining when the population age-structure attained the stable age distribution. In subsequent years, the number of females in each age class will likely increase at a rate equal to λ (assuming current λ is maintained).

It is possible that the 2008 census contained errors in counts of 2- and 3-year-olds, which I distinguished as 'young' individuals with confidence, as a result of field aging techniques. However, because an individual could be considered young for only two years (one year as a 2-

year-old and one year as a 3-year-old), I was able to re-classify individuals incorrectly assigned as young for three years using field-age observations from 2010. By 2010, all 2-year-olds were foals from the 2008 cohort. Thus, my data for 2010 age-structure contained minimal error.

I found that changes in the total number of foals, yearlings, 2- and 3- year-olds varied more than adults. This trend may have been due to a combined influence of varying survival probabilities for different aged individuals (McPeek and Kalisz 1993, Gaillard et al. 1998, Clutton-Brock and Coulson 2002) and the duration of time spent in each age-class. In my life-cycle model, each individual could be a foal, yearling, 2- or 3-year-old for only one year, regardless of survival, while time spent as an adult was limited by an individual's longevity. That the adult age class had the highest number of females in each year may also have contributed to this trend.

Variation in age-distribution is expected in age-structured populations where relative survival and fertility differs between age classes (Clutton-Brock and Coulson 2002, Harris et al. 2008), particularly for ungulates where adult survival remains constant over time and juvenile survival varies with stochastic environmental factors (Gaillard et al. 1998, 2000). For Sable Island horses, I expected the age distribution to vary more between years in number of individuals that are more vulnerable to mortality (i.e., foals, yearlings). This trend fits well with my results and could explain temporal variation in age-distribution which I observed during my study.

Three-year-olds and adults were the only females who produced foals, and these age classes were predicted to have the greatest potential to contribute to future population size. During both years, 3-year-olds had greater reproductive values compared to adults, which may be due to demographic stochasticity resulting in higher fertility of 3-year-olds compared to adults. Given that a female must survive to the birth pulse to reproduce, it is possible that higher survival rates of 3-year-olds contributed to higher reproductive values (as compared to adults).

2.4.2 Current and future population dynamics

Consistent with other ungulates (e.g., Raithel et al. 2005 for elk; Johnson et al. 2010 for Sierra Nevada bighorn sheep), I predict that future λ for the Sable Island horses will be most influenced by proportional changes in adult survival compared to changes in all other vital rates. In general, the influence of changes in fertility on λ is lower than changes in survival. The relative influence

of a vital rate on λ is determined by both its elasticity value and by how much that rate varies temporally (Caswell 1997, Gaillard et al. 2000, Raithel et al. 2007). I observed a pattern which suggested that the vital rate that had highest elasticity value (i.e., adult survival) varied little between years, while vital rates that had lower elasticity values (i.e., adult fertility and foal survival) showed the most variation. This agrees well with many large-bodied mammal populations where rates associated with early life events (i.e., reproduction and juvenile survival) have low elasticity values and high temporal variability, while rates associated with events later in life (i.e., adult survival) have high elasticity values and low temporal variability (e.g., Gaillard et al. 1998 and 2000, Albon et al. 2000 for red deer, Garrott et al. 2003 for elk, Coulson et al. 2005 for red deer, Johnson et al. 2010 for Sierra Nevada bighorn sheep).

Contrary to what might be predicted from elasticity values, my retrospective analysis found the slightly greater $\lambda^{2009-2010}$ was most influenced by changes in adult fertility and foal survival, not adult survival, which ranked highest in analytical elasticity. This agrees with my original prediction. Although, increases in adult fertility made a larger contribution to $\lambda^{2009-2010}$ compared to increases in 3-year-old fertility, which was consistent elasticity values. $\lambda^{2009-2010}$ was only slightly greater than $\lambda^{2008-2009}$, likely because largest contributions were made by vital rates (adult fertility and foal survival) which ranked relatively low in elasticity values. Therefore, small variation in λ can be expected for the population when vital rates with high elasticity values remain relatively constant over time. For example, adult survival remained high and relatively constant between 2008 and 2010, and so there was a small difference in growth between the two years. However, if adult survival were to show the most variation between two years, differences in annual λ would be greater. Similar patterns of vital rate contributions to temporal variation in λ have been observed in other populations of ungulates (e.g., Albon et al. 2000 for red deer, Raithel et al. 2007 for elk), large-bodied mammals (e.g., Brault and Caswell 1993 for orcas *Orcinus orca*), and birds (e.g., Sæther and Bakke 2000 for review).

The population may be fluctuating around a stable equilibrium, where current λ may be maintained in the absence of immigration from outside of the system, predation pressure, and human management. However, in a predator-free environment it is unlikely for an ungulate population to exist in equilibrium with its environment as food resources often limit factor on λ (Sæther 1997). Because of the delayed response in vital rate variation to changes in environmental conditions (Peterson et al. 1984, Couslon et al. 2004, Jacobson et al. 2004), any

evidence of a dynamic equilibrium for an ungulate population cannot be maintained indefinitely as numbers increase and food becomes scarce (see Sæther 1997 for review). This explanation seems more appropriate for future population dynamics of the horses, given that food availability is limited to the amount of forage produced by the island. Therefore, it is doubtful that current population growth will be sustained (McPeek and Kalisz 1993, Caswell 1997, Sæther 1997) as numbers continue to increase and food resources become limited.

2.4.3 Conclusion

Annual variation in λ for the Sable Island horses was small because variation was highest in vital rates (adult fertility and foal survival) which have small elasticity values. The population experienced growth during both years because survival and fertility rates were high for all age classes. A lack of predation pressure and management by humans are possibly contributing factors for the high survival rates. My results suggest that the population was growing at a rate (λ) that had been sustained for some time. However, considering current population size (484 in 2010) and total island area, it is highly unlikely that the current growth rate will continue to be sustained into the future. No population grows *ad infinitum*.

Table 2.3.1. Female horse annual vital rate estimates for each age class used in analyses (2008−2009 and 2009−2010). Survival and fertility rates are presented as [§]mean with [ϕ]95% CI.

2008−2009					
Vital rate		[Ψ]*n*	Lower limit	Mean	Upper limit
Survival	Foal	37	0.784	0.893	0.977
	Yearling	17	0.706	0.886	1.000
	2-year-old	34	1.000	1.000	1.000
	3-year-old	18	0.810	0.943	1.000
	Adult	84	0.848	0.916	0.975
Fertility	3-year-old	18	0	0.269	0.681
	Adult	84	0.152	0.215	0.279
2009−2010					
Vital rate		*n*	Lower limit	Mean	Upper limit
Survival	Foal	31	1.000	1.000	1.000
	Yearling	33	0.800	0.909	1.000
	2-year-old	15	0.786	0.932	1.000
	3-year-old	34	0.844	0.942	1.000
	Adult	94	0.865	0.925	0.973
Fertility	3-year-old	34	0.151	0.330	0.530
	Adult	94	0.200	0.311	0.431

Notes: [§]Mean vital rate values were estimated from 1000 bootstrap resampled data sets for each year using

[ϕ]95% CIs were calculated using the percentile method (2.5% and 97.5% values of bootstrap distribution).

[Ψ]*n* is the number alive post-birth pulse at time *t* for each year.

Variation in age class specific survival: Foal = $2.862e^{-3}$; yearling = $1.320e^{-4}$; 2-year-old = $1.156e^{-3}$; 3-year-old = $2.500e^{-7}$; adult = $2.030e^{-5}$.

Variation in age class specific fertility: 3-year-old = $9.300e^{-4}$; adult = $2.304e^{-3}$.

Table 2.3.2. [¤]Census age-distribution proportions and [§]mean predicted stable age distribution with [ϕ]95% CI for female horses during each year (2008−2009 and 2009−2010).

2008−2009					
		Census proportions	Estimated		
	[Ψ]*n*		Lower limit	Mean	Upper limit
Foal	31	0.150	0.108	0.136	0.168
Yearling	33	0.160	0.091	0.114	0.137
2-year-old	15	0.072	0.074	0.094	0.115
3-year-old	34	0.164	0.071	0.089	0.106
Adult	94	0.454	0.487	0.567	0.649
2009−2010					
		Census proportions	Estimated		
	n		Lower limit	Mean	Upper limit
Foal	45	0.188	0.130	0.161	0.189
Yearling	31	0.130	0.120	0.144	0.164
2-year-old	30	0.126	0.098	0.117	0.134
3-year-old	14	0.059	0.081	0.097	0.111
Adult	119	0.498	0.416	0.482	0.562

Notes: [¤]Census age-distribution proportions are calculated from post birth-pulse census at time *t* +1 for each year.
[§]Mean stable age distribution proportions were estimated from 1000 resampled matrices for each year using bootstrap methods.
[ϕ]95% CIs were calculated using the percentile method.
[Ψ]*n* is the number alive post-birth pulse at time *t* +1 for year.

Table 2.3.3. Female horse annual reproductive value estimates for each age class (2008−2009 and 2009−2010). Reproductive values are presented as [§]mean with [ϕ]95% CI. Foal values are rescaled to 1 making all values comparable.

2008−2009			
	Estimated		
	Lower limit	Mean	Upper limit
Foal	1	1	1
Yearling	1.075	1.196	1.352
2-year-old	1.193	1.450	1.805
3-year-old	1.236	1.544	1.929
Adult	1.041	1.466	1.987
2009−2010			
	Estimated		
	Lower limit	Mean	Upper limit
Foal	1	1	1
Yearling	1.061	1.117	1.170
2-year-old	1.212	1.377	1.578
3-year-old	1.372	1.659	2.002
Adult	1.234	1.621	2.076

Notes: [§]Mean reproductive values were estimated from 1000 resampled matrices for each year using bootstrap methods.
[ϕ]95% CIs were calculated using the percentile method.

Table 2.3.4. Female horse annual elasticity values for each vital rate (2008−2009 and 2009−2010). Elasticity values are presented as [§]mean with [ϕ]95% CI.

2008−2009				
		Estimated		
Vital rate		Lower limit	Mean	Upper limit
Survival	Foal	0.074	0.100	0.132
	Yearling	0.074	0.100	0.132
	2-year-old	0.074	0.100	0.132
	3-year-old	0.067	0.083	0.098
	Adult	0.385	0.518	0.631
Fertility	3-year-old	0	0.017	0.049
	Adult	0.067	0.083	0.098
2009−2010				
		Estimated		
Vital rate		Lower limit	Mean	Upper limit
Survival	Foal	0.093	0.113	0.133
	Yearling	0.093	0.113	0.133
	2-year-old	0.093	0.113	0.133
	3-year-old	0.078	0.093	0.105
	Adult	0.371	0.453	0.549
Fertility	3-year-old	0.008	0.021	0.037
	Adult	0.078	0.093	0.105

Notes: [§]Mean elasticity values were estimated from 1000 resampled matrices for each year using bootstrap methods.
[ϕ] 95% CIs were calculated using the percentile method.

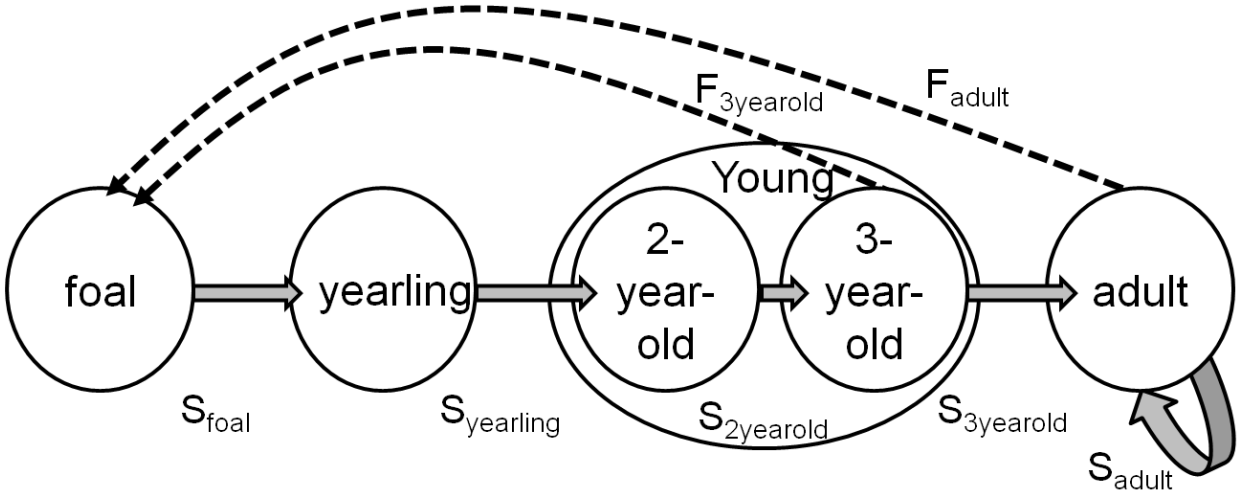

Figure 2.2.1. Age classified life-cycle graph with five age classes for female Sable Island feral horses. Age classes reflect different life-history stages of female horses: (1) foal (0-years-old), (2) yearling (1-year-old, pre-breeder), (3) 2-year-old (pre-breeder of reproductive age), (4) 3-year-old (females generally producing a foal for the first time), and (5) adult (females of prime age and possible senescence). S_i are age-specific survival probabilities and F_i are age-specific fertilities. Transitions between age classes occur once per year.

(a) $A = \begin{pmatrix} 0 & 0 & 0 & F_{3yearold} & F_{adult} \\ S_{foal} & 0 & 0 & 0 & 0 \\ 0 & S_{yearling} & 0 & 0 & 0 \\ 0 & 0 & S_{2yearold} & 0 & 0 \\ 0 & 0 & 0 & S_{3yearold} & S_{adult} \end{pmatrix}$

(b) $A^{2008\text{-}2009} = \begin{pmatrix} 0 & 0 & 0 & 0.269 & 0.215 \\ 0.893 & 0 & 0 & 0 & 0 \\ 0 & 0.889 & 0 & 0 & 0 \\ 0 & 0 & 1.000 & 0 & 0 \\ 0 & 0 & 0 & 0.943 & 0.916 \end{pmatrix}$

(c) $A^{2009\text{-}2010} = \begin{pmatrix} 0 & 0 & 0 & 0.330 & 0.311 \\ 1.000 & 0 & 0 & 0 & 0 \\ 0 & 0.909 & 0 & 0 & 0 \\ 0 & 0 & 0.932 & 0 & 0 \\ 0 & 0 & 0 & 0.942 & 0.925 \end{pmatrix}$

Figure 2.2.2. Post-birth pulse transition matrices for each year of the study parameterized with mean age class survival and fertility rates estimated from bootstrap methods. (a) General matrix structure indicating location of survival and fertility rates for (b) and (c), survival and fertility rate notations are: foal survival (S_{foal}); yearling survival ($S_{yearling}$); 2-year-old survival ($S_{2yearold}$); 3-year-old survival ($S_{3yearold}$); adult survival (S_{adult}); 3-year-old fertility ($F_{3yearold}$); and adult fertility (F_{adult}). (b) 2008-2009 projection matrix; (c) 2009-2010 projection matrix.

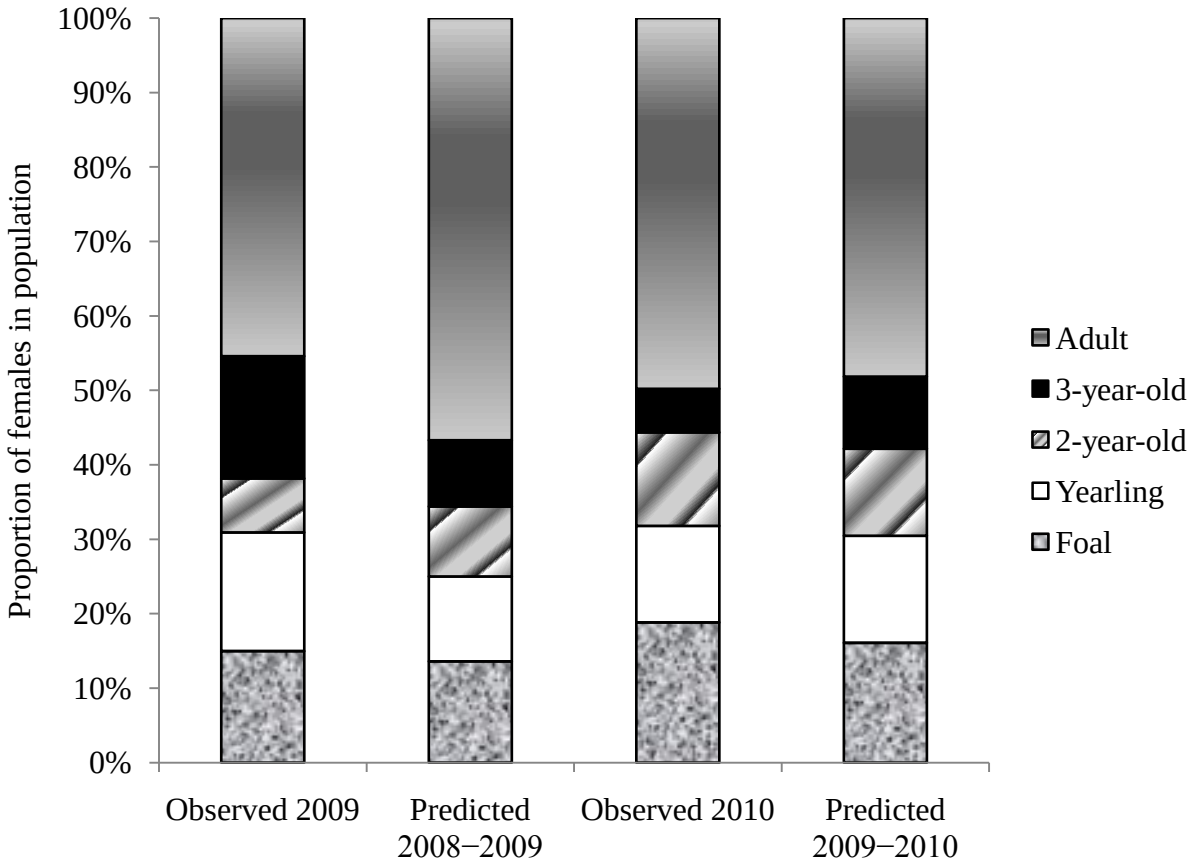

Figure 2.3.1. Observed post-birth pulse census age-structure (2009 and 2010) and predicted stable age distribution for the female portion of the population (2008−2009 and 2009−2010). Predicted stable age distributions are estimated from 1000 resampled matrices using bootstrap methods. Bars show the proportion of females in each age class; age classes reflect life-history stages as in Figure 2.2.1. Observed census age-structure and predicted stable age distribution do not differ for either year (2009 vs. 2008−2009: χ^2 = 0.046, df = 4, P = 0.999; 2010 vs. 2009−2010: χ^2 = 0.013, df = 4, P = 0.999).

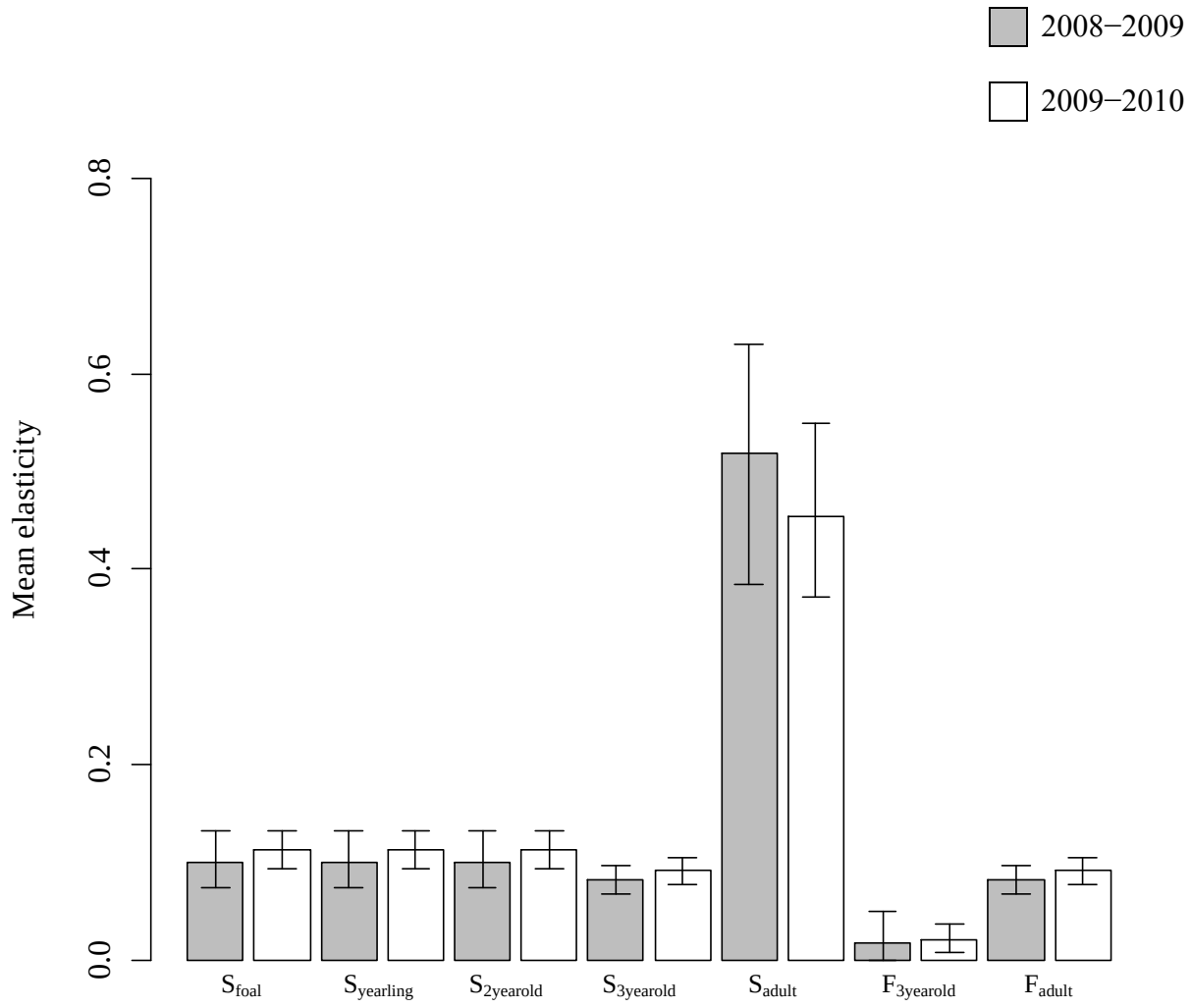

Figure 2.3.2. Mean age class specific vital rate elasticity values and 95% CIs for each year estimated from 1000 resampled matrices using bootstrap methods. Vital rate notations are: foal survival (S_{foal}); yearling survival ($S_{yearling}$); 2-year-old survival ($S_{2yearold}$); 3-year-old survival ($S_{3yearold}$); adult survival (S_{adult}); 3-year-old fertility ($F_{3yearold}$); and adult fertility (F_{adult}). See Table 2.3.4 for 95% CI coordinates.

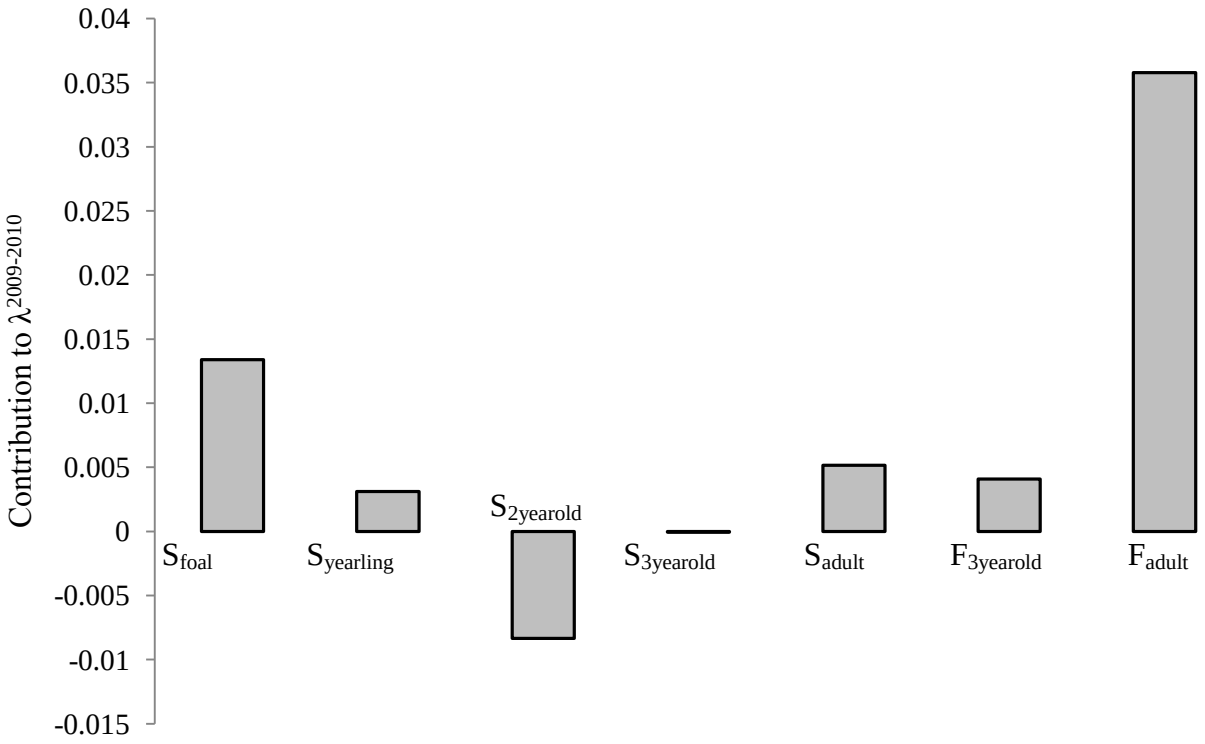

Figure 2.3.3. Contribution that temporal variation in each survival and fertility rate made to the slightly greater λ observed during 2009−2010. Magnitudes of vital rate contributions are listed in Figure 2.3.4 (b). Population growth rates were: $\lambda^{2008-2009} = 1.065$; $\lambda^{2009-2010} = 1.117$; observed difference in growth rates was: $\lambda^{2009-2010} - \lambda^{2008-2009} = 0.052$. Overall contribution values sum to 0.053. Survival and fertility rate notations are: foal survival (S_{foal}); yearling survival ($S_{yearling}$); 2-year-old survival ($S_{2yearold}$); 3-year-old survival ($S_{3yearold}$); adult survival (S_{adult}); 3-year-old fertility ($F_{3yearold}$); and adult fertility (F_{adult}).

(a)

$$\mathbf{C} = \begin{pmatrix} 0 & 0 & 0 & F_{3yearold} & F_{adult} \\ S_{foal} & 0 & 0 & 0 & 0 \\ 0 & S_{yearling} & 0 & 0 & 0 \\ 0 & 0 & S_{2yearold} & 0 & 0 \\ 0 & 0 & 0 & S_{3yearold} & S_{adult} \end{pmatrix}$$

(b)

$$\mathbf{C} = \begin{pmatrix} 0 & 0 & 0 & 0.0041 & 0.0358 \\ 0.0134 & 0 & 0 & 0 & 0 \\ 0 & 0.0031 & 0 & 0 & 0 \\ 0 & 0 & -0.0084 & 0 & 0 \\ 0 & 0 & 0 & -5.1856e^{-05} & 0.0052 \end{pmatrix}$$

Figure 2.3.4. Matrix of contributions indicating contribution made by variation in each vital rate to $\lambda^{2009-2010}$. (a) General matrix structure indicating location of survival and fertility rate contribution values. Survival and fertility rate notations are: foal survival (S_{foal}); yearling survival ($S_{yearling}$); 2-year-old survival ($S_{2yearold}$); 3-year-old survival ($S_{3yearold}$); adult survival (S_{adult}); 3-year-old fertility ($F_{3yearold}$); and adult fertility (F_{adult}). (b) Magnitude of contributions from variation in age class specific survival and fertility rates. The elements of C sum to 0.053.

CHAPTER 3: SOURCE-SINK DYNAMICS: IMMIGRATION AND EMIGRATION BETWEEN THREE AREAS AS AN EXPLANATION FOR SPATIAL HETEROGENEITY IN POPULATION GROWTH

3.1 INTRODUCTION

Within an animal population's geographic range, heterogeneity in landscape characteristics can cause spatial substructure where groups, or subunits, of individuals experience different levels of habitat quality (Pulliam, Dunning, Jr., and Liu 1992, Amarasekare 1994, Maurizen et al. 2002, Naranjo and Bodmer 2007). Habitat quality can be determined from several landscape characteristics including primary productivity (Marshall 2009, Mobæk 2009), predation or hunting pressure (Holt 1985, Naranjo and Bodmer 2007), conspecific density and mating opportunities (Pulliam 1988, McPeek and Holt 1992), or water quality and availability (Rubenstein 1994, Virgl and Messier 2000). Population subunits that occupy good-quality habitats tend to have area-specific advantages in fitness (i.e., high survival and reproduction), compared to subunits in poor-quality habitats. Contrasting survival and reproduction rates are predicted to cause a surplus of individuals in good-quality habitats (where births exceed deaths), and a deficit of individuals in poor-quality habitats (where deaths exceed births; Pulliam 1988, Delibes, Gaona, and Ferreras 2001). For example, high birth rates in good-quality meadows led to a consistently higher population size for American pikas (*Ochotona princeps*, Lagomorpha) compared to those in snowbeds, where birth rates and λ was below replacement (Kreuzer and Huntly 2003). Given the ability of animals to actively select between habitats (Holt 1985, Fretwell and Lucas 1969, Mobæk et al. 2009), individual movements between subunits should have a considerable influence on local demography (Hanski 2001, Kreuzer and Huntly 2003), and may lead to spatial heterogeneity in population growth (Pulliam 1988, Pulliam et al. 1992, McPeek and Kalisz 1993, Coulson et al. 1997).

Pulliam's (1988) source-sink model has been used to explain how differences in demographic rates between subunits influence population growth and regulation. In his model, 'sources' are highly productive subunits that contain a surplus of individuals; conversely, 'sinks' contain a deficit of individuals due to below replacement birth rates. Pulliam was the first to suggest that surplus individuals choose to leave sources when their perceived reproductive success is higher is a sink, thus maintaining sink subunits in an evolutionarily stable process. Since then, much work has focused on determining the role that sinks play in population-level growth rate (Howe et al. 1991, Watkinson and Sutherland 1995, Thomas and Kunin 1999, Delibes et al. 2001, Robinson et al. 2008, Cooley et al. 2009, Zeigler et al. 2010). For example, Doak (1995) demonstrated that population viability of Yellowstone grizzly bears (*Ursus arctos*

horribilis) decreased with increasing movement of individuals from good (i.e., low degradation) to poor (i.e., high degradation) habitats. Foppen et al. (2000) associated movement of reed warblers (*Acrocephalus scirpaceus*) from source areas to low density sink areas with increased stability of source subunits. Naranjo and Bodmer (2007) found that losses from a locally overhunted population of red brocket deer (*Mazama americana*) were augmented by immigration from an adjacent source population. However, few studies have quantified the realized influence of emigration and immigration on subunit-specific survival, reproduction, and growth (Watkinson and Sutherland 1995, Virgl and Messier 2000, Zachariah Peery et al. 2006).

Understanding the influence of emigration and immigration on subunit-specific demography is a goal that can only be accomplished by following movements of marked individuals, particularly in a closed system, where all possible residents and migrants are known. Without accurately recording the age, sex, and number of individuals that move between ecologically distinct areas, it is not possible to determine the realized influence of immigration and emigration on subunit-specific demography. For example, at times even sink subunits might experience growth or stability ($\lambda \geq 1$) when immigrants enter from other subunits (Thomas and Kunin 1999, Delibes et al. 2001, Johnson 2004, Zachariah Peery et al. 2006) and balance sink-related deaths through a process similar to the rescue-effect (Hanski 2001, Robinson et al. 2008).

Here I identify spatially distinct, but open (i.e., subject to immigration and emigration), population subunits for the Sable Island horses along a habitat gradient defined by surface water availability. Heterogeneity of water resources reflects varying habitat quality (on Sable Island: Catling et al. 1984, also see: Virgl and Messier 2000) and may influence female spatial distribution and movement patterns, as seen in horses and other ungulate populations (e.g., Rubenstein 1981 and Berger 1986 for feral horses; Ritter and Bednekoff 1995 for Springbok *Antidorcas marsupialis*; Marshal et al. 2006 for mule deer *Odocoileus hemionus eremicus*; Chamaillé-Jammes, Valeix, and Fritz 2007 for African elephant *Loxodonta africana*). Spatial heterogeneity of water on Sable Island presented me with an opportunity to assess source-sink dynamics within a continuous population range, while accounting for individual immigration and emigration events. I monitored movement of females (98.7% of females of all ages) and assigned source-sink status to subunits by determining: (1) the influence of immigration on subunit-specific λ using methods modified from Zachariah Peery et al. (2006), (2) annual emigration and immigration rates for each subunit using methods modified from Virgl and

Messier (2000), and (3) how emigration rates change with changes in local density for each subunit using theory modified from Pulliam (1988).

If females perceive areas near permanent pond water sources as high quality habitat, I predict that source subunits will be found in areas with high surface water availability. Source subunits should show an increasing population trend where local birth rates compensate for losses due to death and emigration; therefore, a surplus of individuals should be found in source subunits. If females leave areas of high density in search of mating opportunities (Pulliam 1988, Virgl and Messier 2000) or to reduce competition, then emigration rates of reproductive-aged females should be higher for source subunits as local density increases. Likewise, immigration rates into source subunits should be low, and any immigrants should have little influence on a source subunit's growth rate (Thomas and Kunin 1999, Zachariah Peery et al. 2006). On the other hand, I expect to find a deficit of individuals in sink subunits where low birth rate and/or high mortality of residents should cause a decreasing population trend. Changes in local density for sink subunits should be more variable compared to source subunits, although I do not expect to find this association for sink areas (Pulliam 1988; Howe et al. 1991). Because surplus individuals should leave source subunits and immigrate into sink subunits, I expect that immigration rates into sink subunits will be high; any immigrants should have a considerable influence on a sink subunit's growth rate (Thomas and Kunin 1999, Zachariah Peery et al. 2006).

3.2 METHODS

3.2.1 Source-sink subunits

3.2.1.1 Spatial heterogeneity of island area

I characterized the availability of water to horses along a longitudinal gradient (Figure 3.2.1). In the west, horses have access to permanent water. However, in the central and more eastern areas of the island, the number and total surface area of permanent ponds declines. In the far-east, shallow water ponds disappear during the summer months (Lucas et al. 2009). Here, more than anywhere else on the island, horses dig into the sand to access water (Figure 3.2.1). Digging behaviour is not usually observed at the far-west areas (personal observation). I chose to stratify the population spatially using water resources because water availability reflects varying habitat

quality, and influences the distribution of females in polygynous mating systems, especially during the summer months (e.g., Ritter and Bednekoff 1995 for springbok; Virgl and Messier 2000 for muskrat *Ondatra zibethicus*). For example, Moehlman (1998) found that females with young foals in a population of feral asses (California, USA) remained closer to a water source and drank on average two to three times a day compared to once by other individuals. During their first three months, foals did not drink free-standing water and relied on their mother for fluids; thus, lactating females were under higher water stress compared to individuals without foals during the post-birth period. Similar spacing and drinking behaviour has been observed in other species of equids for females with offspring (see Rubenstein 1994 for feral horses, Plains Zebra *Equus burchelli*, Grevy's Zebra *Equus grevyi*, and Onager *Equus hemionus*), and therefore could limit the spatial distribution of females on Sable Island during summer months.

I used locations where individuals obtained water as the basis for spatially stratifying the population into distinct subunits. I collected location data for permanent water pond and hole sources during daily censuses (see Chapter 1.2.3), and used polythetic agglomerative hierarchical cluster analysis (HCA) to group Cartesian locations (n = 122). HCA was selected because it accurately identified spatially distinct water groups nested within the total population of water resources (Coulson et al. 1997; McCune and Grace 2002). Starting with all water locations as separate points, HCA formed groups by fusion based on similarity of locations (McCune and Grace 2002). I used a Euclidean distance dissimilarity matrix calculated from unstandardized location data because I was interested in grouping water resources based on space, in terms of scale and dimensions, and standardization would remove this information (Kenkel 2006). I grouped water resources using average-linkage (Coulson et al. 1997; Mauritzen et al. 2002). HCA produced a dendrogram illustrating the strength of the group solution; the most appropriate number of water resource groups was determined from a *K*-means analysis (Van Sickle 1997; McCune and Grace 2002). The appropriateness of selected clusters was confirmed visually by projecting water resource groupings as a layer using a Geographical Information System (GIS, Appendix C, Figure C.3.2.1). I used locations of females using a particular water group to extrapolate from water resource substructure and define area boundaries.

3.2.1.2 Subunit residency

For each field season, I used 3−11 GPS locations collected for each female to assign subunit residency. I assigned residency to females that were situated within the boundary of a specific area.

3.2.2 Subunit-specific demography

3.2.2.1 Losses and gains

Annual demographic parameters for each subunit were influenced by births, deaths, immigration, and emigration. To understand how losses of individuals not related to resident deaths affected subunit-specific survival, I estimated survival rates from losses in the absence and presence of emigration. To understand how gains of individuals not related to resident births affected subunit-specific fertility, I estimated gains from resident fertility rates at $t + 1$ in the absence and presence of immigration.

I assessed losses and gains from the presence and absence of females within each subunit. My sampling protocol (see Chapter 1.2.3) included comprehensive monitoring of females, and so I was able to assign a mortality event to a female that was absent from my annual island-wide censuses with very high confidence. I used log-linear models to test whether demographic rates differed between subunits for years 2008−2009 and 2009−2010 (Virgl and Messier 2000, Caswell 2001).

I identified annual (t to $t + 1$) immigration and emigration events as the movement of individuals from one subunit to another, e.g., from summer 2008 to summer 2009. Movements occurred almost exclusively outside of the census months (I observed the migration of one band, consisting of one adult female, two 3-year-old females, and one yearling female while collecting 2010 summer census data). I assumed that immigration and emigration events occurred after the census of year t, but before the breeding season of year $t + 1$. For example, during the first year (2008−2009), a female observed in subunit i at time t, that was observed in subunit j at time $t + 1$, was considered to have emigrated from subunit i and immigrated into subunit j after the winter (t), but before the breeding season ($t + 1$). As a result, a female observed with a foal during census at $t + 1$ immediately following immigration was assumed to have mated in the subunit

from which she emigrated. If mortality occurred during or after a movement event, but before my census period in a given year, I was only able to assign mortality the subunit from which a migrant originated.

Losses

I estimated losses due to mortality for each subunit following methods outlined in Chapter 2.2.3.1. My survival calculation considers foal survival, in addition to all other age classes, over the 'winter' period. There was virtually no summer mortality (i.e., occurring during the time I conducted censuses).

For each subunit, I estimated annual age class survival rates in the absence of emigration as the proportion of residents from censuses at t that were alive at $t + 1$. This method corrected for losses due to emigration by assuming that a female emigrant observed at $t + 1$ survived the winter in the area she was found in at t and then moved (Virgl and Messier 2000). I then estimated age class survival rates in the presence of losses due to deaths and emigration. Here, survival was the proportion of residents from censuses at t that were observed alive in the same subunit at $t + 1$ for each year.

Gains

I used individual fertility rates as a proxy for reproduction (see 2.2.3.1). I defined annual fertility as the number of surviving foals a female of age-class i produced by post-birth censuses at $t + 1$ (see Chapter 2.2.3.1). I used a post-birth pulse calculation to assign each female a fertility value. Individual fertility values equalled a female's age class survival probability for the year, t to $t + 1$, times the number of yearlings she was expected to contribute to the next year's census at t (Caswell 2001, Morris and Doak 2002, Iverson and Esler 2010). Age class fertility rates were calculated as the average of individual fertility values of females in each age class.

I was able to determine which foals belonged to residents and which belonged to immigrants each year. I calculated age class fertility values for residents at $t + 1$, without considering births from immigrants, as an average of individual fertility values of residents. I then estimated age class contributions made to resident birth rates by immigrants as an average of individual fertility values of immigrants. I compared resident and immigrant fertility rates to determine how fertility in each subunit changed in the presence of immigration.

For the 2010 birth pulse, I could determine if a 2009 immigrant that had established residency in a subunit contributed to the 2010 birth rate by reproducing. I counted births for all

2009 immigrants who had become residents in 2010. I compared counts between subunits to determine if immigrants continued to contribute to a subunit's birth rate in subsequent years.

3.2.2.2 Body condition

Body condition is a reliable method for ranking individual quality for various species of equids because it affects both survival and reproduction (Rubenstein 1981, Cameron et al. 1999, Cameron and Linklater 2007). I assigned each female ≥2 years old a body condition score at each observation following methods described in Chapter 1.2.3.2. To evaluate the basis of potential differences in survival and fertility among subunits, I tested for differences in annual post-birth pulse body condition of females that used different water resource groups (i.e., residents of different subunits). I used a Mann-Whitney *U* test (Siegel and Castellan, Jr. 1988) because body condition scores were based on an ordinal and discrete 11-point scale (Carroll and Huntingdon 1988, Cameron et al. 1999).

3.2.2.3. Temporal variation in subunit population size and local density

I estimated post-birth pulse population size for each subunit from minimum count data collected during annual censuses, following the whole-island census method described in Chapter 1.2.3. Local density was determined from annual subunit population size as the total number of females per kilometre square of vegetated surface area.

3.2.2.4. Subunit-specific population growth rate

I estimated time-specific, realized rate of population increase (λ_C) for each subunit from census counts of females. I used the formula: N_{t+1}/N_t to estimate λ_C for the first (t = 2008) and second (t = 2009) years of my study. Because λ_C is calculated from total counts, values consider birth, death, emigration, and immigration for each subunit (Zachariah Peery et al. 2006). A λ_C value >1 indicated that the subunit expanded in population size, a λ_C value <1 indicated the subunit decreased in size, and a λ_C value = 1 indicated the subunit population size remained stable (Caswell 2001).

3.2.3. Influence of immigration on subunit growth

To determine the time-specific influence of immigration, I estimated subunit-specific population growth rates in the presence and absence of immigration following Zachariah Peery et al. (2006). I used the realized rate of population increase (λ_C) to represent subunit population growth in the presence of immigration (see 3.2.2.4). I estimated population growth rate in the absence of immigration (λ_M) using a projection matrix model (Caswell 2001) parameterized with resident age class survival (where emigration was considered as death) and fertility rates.

I constructed six age-class structured matrix models (Leslie 1945) to determine λ_M for each subunit during each year. I constructed matrix models following methods outlined in Chapter 2.2.3. Models used in analyses were linear, time invariant population projection matrix models (McPeek and Kalisz 1993, Caswell 1997), which described dynamics of the female portion of the population only. Projection interval for each model was one year. I estimated resident age class survival and fertility rates in the presence of emigration (i.e., emigrants considered as deaths for each subunit) as explained in 3.2.1.

Because λ_C considered birth, death, emigration, and immigration, and λ_M only considered births, deaths, and emigration (i.e., incorporates apparent survival) for each subunit, λ_C will always be $\geq \lambda_M$. I used the difference between λ_C and λ_M to assess the influence of immigration on subunit growth and to predict how growth trends would respond to decreased immigration (Zachariah Peery et al. 2006). If $\lambda_C = \lambda_M$ a subunit received no immigrants during a given year.

I used the following rationale (i−v), based on Zachariah Peery et al. (2006), to determine subunit growth trends in the presence and absence of immigration:

i. When λ_C and λ_M are < 1, a subunit is declining in size. $\lambda_C - \lambda_M$ will be > 0 indicating the subunit received immigrants, but because growth was declining, immigration did not balance losses due to resident mortality and emigration. If immigration were to decrease, a faster rate of decline should occur.

ii. When λ_C is ≥ 1 but λ_M is < 1, a subunit is stable or increasing in size. $\lambda_C - \lambda_M$ will be > 0 and indicate the subunit received immigrants. Here, immigrants augmented negative growth (λ_M <1). If the subunit was stable (i.e., $\lambda_C = 1$), immigration had a slight influence on growth; if the subunit increased in size, immigration had a greater influence on growth. If immigration were to decrease, a decline is expected.

iii. When λ_C and λ_M = 1, a subunit is stable in size. $\lambda_C - \lambda_M$ will = 0 and indicate the subunit received no immigrants. As immigration did not occur, a decrease in immigration should have no effect on stability.

iv. When λ_C is > 1 and λ_M is = 1, a subunit is increasing in size. $\lambda_C - \lambda_M$ will be > 0 and indicate the subunit received immigrants. Because population size is expected to be stable in the absence of immigration (λ_M = 1), immigration influenced growth. If immigration were to decrease, stability is expected.

v. When λ_C and λ_M are > 1, a subunit is self-sustaining. A $\lambda_C - \lambda_M$ value = 0 indicates no immigration, and no influence of decreased immigration growth. However, a $\lambda_C - \lambda_M$ value > 0 indicates the subunit may have received immigrants which contributed to growth. If immigration were to decrease, a slower increase is expected.

In the absence of immigration, it is possible that temporal variability in resident fertility may result in birth rates exceeding losses due to resident mortality and emigration. Under these circumstances, the realized rate of increase for a subunit may suggest growth (λ_C > 1), while the estimated rate of population change may suggest stability (λ_M = 1). The difference between λ_C and λ_M ($\lambda_C - \lambda_M$ > 0) would suggest that immigration influenced growth, even though none occurred. If this took place for any subunits, I might have incorrectly attributed growth to an influence of immigration without verifying that immigration actually occurred. To prevent such error, I considered annual immigration rates, in addition to the relationship between λ_C and λ_M, when determining the influence of immigration on subunit-specific population growth.

3.2.4. Subunit age class immigration and emigration rates

To verify if each subunit received immigrants and produced emigrants, I estimated annual age class immigration and emigration rates for each subunit. Immigration and emigration events were identified during post-birth pulse censuses at the end of each year (t + 1), as outlined in 3.2.2.1. I did not consider the movement of the single band I observed moving between subunits during 2010 because this event occurred at the end of the season, and I was unable to determine which subunit the band immigrated to.

I estimated age class immigration and emigration rates for each m subunit from t to t + 1 following Virgl and Messier (2000). Immigration rates were estimated as: $I/(R_{t+1} + I)$; where I is the number of immigrants in subunit m at t + 1 and R_{t+1} is the number of residents alive in

subunit *m* at *t* + 1. Emigration rates were estimated as: $E/(R_t + E)$; where E is the number of emigrants from subunit *m* that left prior to censuses at *t* + 1 and R_t is the number of residents alive in subunit *m* at *t*.

I compared annual emigration and immigration rates, independently, between subunits using χ^2 analysis to determine if any subunit produced more emigrants, or received more immigrants, than expected by chance. For the χ^2 analysis, I assumed that all subunits had equal probability of (1) producing emigrants and (2) accepting immigrants.

3.2.5. Local density and subunit-specific emigration rates

High survival and reproduction are predicted to cause greater local density in sources compared to sinks (Pulliam 1988). As source density increases, mating opportunities and habitat resources become limited, and surplus individuals move into sink areas where density and competition is lower (Pulliam 1988, Virgl and Messier 2000). I determined the association between changes in local density and emigration rates by comparing annual subunit-specific emigration rates of reproductive aged females to changes in local density. I pooled emigration rates of 2-year-olds (see Chapter 1.2.2.6), 3-year-olds, and adults into one category representing females of reproductive age. I assumed that every female had an equal probability of mating in each subunit. Therefore, no age class of reproductive females should be more likely to emigrate than the others.

3.2.6. Subunit status

I assigned source or sink status to each subunit using criteria selected from Pulliam (1988), Virgl and Messier (2000), and Zachariah Peery et al. (2006) (Table 3.2.1).

3.2.7. Statistical analyses

I used the R package popbio (Stubben and Milligan 2007, R Core Development Team 2010) to calculate λ_M for each subunit. I used the R package MASS (Venables and Ripley 2002) to perform log-linear analyses. All other statistical analyses were performed using R base package (R Development Core Team 2010). For all statistical tests, I employed an alpha value of 0.05.

3.3 RESULTS

3.3.1 Source-sink subunits

3.3.1.1 Spatial heterogeneity of island area

A HCA and a *K*-means analysis suggested three distinct water resource groupings (see Appendix C, Figures C.3.3.1 and C.3.3.1, respectively). Female proximity to water groups defined geographical borders for three neighbouring island areas (Figure 3.3.1). No female was observed using more than one water grouping during any year.

Area 1 was located on the west side of the island and had smaller surface area (7.891 km^2) when compared to Area 2 (central; 13.260 km^2) and Area 3 (east side; 8.786 km^2). Total vegetated land cover in each area followed a similar pattern: Area 1 had the smallest vegetated area (3.691 km^2), compared to Area 2 (7.317 km^2) and Area 3 (3.867 km^2). There was a distinct pattern of water type and availability between areas. Area 1 contained only ponds covering a surface area of 0.122 km^2; Area 2 contained some centrally located ponds covering a surface area of 0.096 km^2 and some holes; and Area 3 contained no ponds and horses used only holes (area data from Muise 2011).

3.3.1.2. Subunit residency

Each area contained one population subunit. I observed 22 individual immigration events between subunits during my study (2009 and 2010 post-birth pulses). However, most females tended to remain in previously occupied areas in subsequent years.

3.3.2. Subunit-specific demography

3.3.2.1 Losses and gains

Emigration-corrected survival did not vary for any subunit (Table 3.3.1.A). Log-linear models indicated that survival rates were not significantly different for residents in each age class (Table 3.3.1.A, $G^2 = 5.796$, df = 4, $P = 0.21$). During each year, foal, yearling, and 3-year-old emigration-corrected survival was highest in subunit 3; there was little variation between subunits for 2-year-old survival. Adult survival varied the most between subunits and years, but

tended to be highest in subunit 1 (Table 3.3.1.A). Emigration events outside of the birth-pulse influenced subunit-specific survival rates (Table 3.3.1.A vs. Table 3.3.2.B). When emigration was considered as death, there was a noticeable change in survival rates for subunits 1 and 3, but little change in survival rates for subunit 2 (Table 3.3.1.B vs. Table 3.3.1.A). Because survival probabilities for individuals were not different between areas, I was unable to use subunit-specific survival rates as an indicator of source-sink status.

Resident fertility was not distributed equally among areas during year 1 (Table 3.3.1.B, $G^2 = 8.566$, df = 2, $P = 0.014$), which was largely due to combined effects of age class and area. Considered over both years, the effects of age class and area on fertility was just short of significant ($G^2 = 5.614$, df = 2, $P = 0.060$). There was little change in resident fertility in subunit 1 between years. In year 1, fertility was lowest in subunit 3 compared to subunits 1 and 2. However, in the second year fertility in subunit 3 was higher than in subunit 1 or 2 (Table 3.3.1.B). At post-birth pulse counts in each year (i.e., 2009 and 2010), resident females of subunit 1 produced a comparable number of foals; however in 2010, females of subunits 2 and 3 had produced 5 and 8 more foals, respectively (Table 3.3.1.B).

Two 3-year-old immigrants contributed to resident birth rate by reproducing immediately following immigration: one in subunit 1 during 2009 and one in subunit 2 during 2010 (Table 3.3.1.B). By 2010, after immigrants had established residency, one adult female that immigrated to subunit 2 during 2009 reproduced. No immigrants from 2009 contributed to the 2010 birth rate in subunit 1 or 3.

3.3.2.2 Body condition

Over all three years, females living in Area 1 had better body condition compared to females living in Areas 2 (Mann-Whitney *U* test; $P = 0.033$) and 3 (Mann-Whitney *U* test; $p = 0.001$). However, there was no difference in condition between females in Area 2 and 3 (Mann-Whitney *U* test; $P = 0.184$).

3.3.2.3 Temporal variation in population size and local density

Total number of females in each subunit increased during the study (Table 3.3.2), although increases were more variable in subunit 2 compared to 1 and 3. For example, mean (± SD)

increase in population size between 2008 and 2010 for subunit 2 was 15.0 ± 11.3, compared to increases of 8.5 ± 2.1 for subunit 1 and 1.0 ± 1.4 for subunit 3. Subunit 1 contained the largest number of females compared to subunits 2 and 3 (Figure 3.3.2).

3.3.2.4 Subunit-specific population growth rate

Realized rate of population increase (λ_C) indicated that positive population growth occurred in each subunit during both years (Table 3.3.2), excluding stability for subunit 3 in year one. When birth, death, immigration, and emigration were considered, subunit 2 experienced the largest population growth during both years ($\lambda_C^{2008-2009} = 1.130$ and $\lambda_C^{2009-2010} = 1.377$), compared to subunit 1 ($\lambda_C^{2008-2009} = 1.115$ and $\lambda_C^{2009-2010} = 1.073$) and subunit 3 ($\lambda_C^{2008-2009} = 1.000$ and $\lambda_C^{2009-2010} = 1.041$).

3.3.3 Influence of immigration on subunit growth

In the absence of immigration (λ_M), predicted trends for each subunit were less than calculated based on counts of individuals (λ_C; Table 3.3.2). The relationship between λ_C and λ_M indicated that immigration affected population growth each subunit in both years. Subunit 1 had an increasing trend during both years ($\lambda_M^{2008-2009} = 1.050$ and $\lambda_M^{2009-2010} = 1.034$), although the rate of growth was lower than expected from λ_C (Table 3.3.2). Conversely, during the first year, negative growth was predicted for subunit 2 ($\lambda_M^{2008-2009} = 0.951$) and subunit 3 ($\lambda_M^{2008-2009} = 0.932$) in the absence of immigration (Table 3.3.2). However, in year 2, growth trends in the absence of immigration had become positive for subunit 2 ($\lambda_M^{2009-2010} = 1.123$). Subunit 3 did not receive any immigrants in the second year and remained stable ($\lambda_M^{2009-2010} = 0.999$).

3.3.4 Subunit age class immigration and emigration rates

By the end of my study, subunit 2 had a significantly higher ratio of immigrants to residents compared to subunits 1 and 3 ($\chi^2 = 11.686$, df = 2, $P = 0.003$). During 2009, there was no difference in the number of immigrants entering each subunit ($\chi^2 = 2.733$, df = 2, $P = 0.455$); however, subunit 2 and 1 received more immigrants than subunit 3 (Table 3.3.3; five, four, and two immigrants, respectively). Immigration was not equally distributed between subunits during

2010 (χ^2 = 15.916, df = 2, P < 0.050); subunit 2 received significantly more immigrants than subunit 1 (10 and one immigrant, respectively), while subunit 3 received no immigrants.

Over both years, mean (± SE) immigration rates were highest and most variable for subunit 2 (Table 3.3.3; 0.141 ± 0.032), compared to subunit 1 (0.033 ± 0.021) and subunit 3 (0.023 ± 0.023). The rates of 3-year-old and adult immigration were highest for subunit 2 compared to subunit 1 and subunit 3 (Table 3.3.3). For both years, the number of 3-year-old and adult females entering subunit 2 was significantly higher compared to subunits 1 and 3 (2008−2009: χ^2 = 16.412, df = 2, P = 0.003; 2009−2010: χ^2 = 10.502, df = 2, P = 0.005) Immigration rates were consistently highest for subunit 2, while emigration rate were consistently highest for subunits 1 and 3 (Table 3.3.3).

3.3.5 Local density and subunit-specific emigration rates

Changes in local density reflected variability of population increases for each subunit (see 3.2.2.3). Local density was highest in subunit 1, compared to 2 and 3, and showed a steady increase during my study (Figure 3.3.2). Local density of subunit 2 had the most variable increase, although only slightly greater than for subunit 1. Local density of subunit 3 was higher than subunit 2, but increased the least of all three subunits (no change between 2008 and 2009).

Increased local density for subunit 1was associated with increased reproductive aged emigration (Figure 3.3.3 (a)). Slight increases in local density were associated with increased emigration for subunit 3 (Figure 3.3.3 (b)), however increased resident fertility (Table 3.3.1.B) was associated with increased emigration. Emigration for subunit 2 was negatively associated with increased local density (Figure 3.3.2 (c)) and increased resident fertility rates (Table 3.3.1.B).

3.3.6 Subunit status

During my study, subunit 1 behaved as an increasing source, subunit 2 behaved as an increasing sink, and subunit 3 behaved as a stable source (Table 3.3.4).

3.4 DISCUSSION

My primary objective was to determine if spatial heterogeneity in population growth was present on Sable Island. I assessed the existence of source-sink dynamics and identified source subunits which may supplement growth in less productive areas. My results suggested subunit-specific growth trends related to the presence and absence of immigration. I found evidence for an association between emigration and both increasing local density and increasing resident birth rates. These results are consistent with predictions of Pulliam's (1988) source-sink theory. Immigration and emigration events appeared to have a considerable influence on subunit-specific growth and source-sink status.

Local population size increased for each subunit; although, I did find evidence of contrasting trends when immigration was considered. Increases in subunit size complimented current population-level growth (see Chapter 2). Therefore, I consider my results to suggest spatial heterogeneity in population growth on Sable Island: it appears that source-sink dynamics exists between three spatially distinct subunits. Specifically, a productive population source was identified in the west of the island where permanent water ponds occur.

My results are unique given that I was able to distinguish between emigration and mortality for each subunit by monitoring movements of almost every female. As Sable Island is a closed system, immigration of unknown individuals into, or emigration or known individuals out of my study area could not occur, and thus did not complicate my results. Most studies of source-sink dynamics are unable to account for all individual movements (e.g., Amarasekare 1994, Foppin et al. 2000, Kreuzer and Huntly 2003), and so the true influence of immigration and emigration cannot be assessed, and thus is not considered (see: Virgl and Messier 2000, Zachariah Peery et al. 2006, Robinson et al. 2008).

I calculated parameters that are classically used to define sources and sinks, and found that only one subunit (subunit 1) exhibited all characteristics consistent with a 'source.' However, overall, my results suggest that there is spatial heterogeneity in population-level growth. Therefore, it appears that accurately distinguishing between sources and sinks, at least for growing populations similar to the Sable system, cannot be accomplished using only subunit-specific demographic rates or the influence of immigration on growth (Watkinson and Sutherland 1995, Thomas and Kunin 1999). It is possible that other factors, such as (a) differences in fitness between residents or between residents and immigrants, (b) sociality, and

(c) habitat quality, play an integral role in source-sink status. Therefore, the individual monitoring approach I used here may be considered a first step toward understanding the realized influence of immigration and emigration on area-specific demography. I believe that incorporating factors (a−c) into analyses may allow us to uncover the direct consequences of internal source-sink dynamics.

3.4.1 Spatial heterogeneity of island area

There are three areas on Sable Island, defined by different water availability, which support three spatially distinct subunits. Active dispersal between subunits suggests population substructure and spatial heterogeneity in horse distribution. It could be argued that area divisions, and thus subunits, are ambiguous because there are no landscape barriers which might limit movement. In addition, the methods I used to distinguish between areas did not consider forage quality. There are no data on forage quality for Sable Island, and so I was limited in my ability to incorporate any measure other than surface water availability in my methods. However, spatial distribution of water could influence female movements during the summer season, like for other equid females with offspring (see 3.2.1; e.g., Rubenstein 1994 for feral horses, Plains Zebra, Grevy's Zebra, Onager, Moehlman 1998 for feral asses). The majority of females remained in the same subunit during the three years. Complete mixing of subunits did not occur, which suggests that the subunit spatial structure I identified was appropriate for assessing the existence of source-sink dynamics.

The subunits I identified closely mirror previous genetic findings for the population (Lucas et al. 2009). Lucas et al. (2009) used tissue samples from deceased horses to assess genetic diversity at a spatial scale of four equally sized subdivisions (I−IV, west−east); subdivisions divided the island along its length. My analyses placed subunit 1 within western subdivision I. Subunit 2 was located within central subdivisions II and III, and subunit 3 was located within eastern subdivision IV. Lucas et al. (2009) found that horses in subdivision IV had 10% greater heterozygosity compared to horses in western subdivisions (i.e., I, II, and III). This suggested outbreeding in eastern subdivision IV and higher levels of inbreeding in western subdivisions. Outbreeding in subdivision IV is consistent with a spatial distinction between subunit 3 and subunits 1 and 2. Increased effective number of alleles and allelic richness

between subdivisions I and III (Lucas et al. 2009) are consistent with a spatial distinction between subunits 1 and 2.

3.4.2 Source-sink subunit status

Several patterns in my data support the interpretation that subunits 1 and 3 are sources and subunit 2 is a sink. However, distinction of source status for subunit 3, relative to subunit 1, must be clarified. I found that subunit 1 had all characteristics consistent with being a source, while subunit 3 had only the characteristics relating to the effect of emigration on demography, and immigration vs. emigration. Based on λ_M alone, subunit 3 was a sink. However, as no immigration occurred during the second year, realized growth could only be attributed to increased resident fertility (3 foals in 2009 compared to 11 foals in 2010). The effect of demographic stochasticity on changing population size is apparent for this relatively small subunit. Verification that subunit 3 as a true source, or some intermediate population (see below), will be possible with more data during periods with different densities and different levels of emigration and immigration. My data indicate that subunit 3 produced a comparable number of emigrants to subunit 1. As almost all immigrants moved into subunit 2, I consider the behaviour of subunit 3 as a source during my study. However, I was unable to find evidence for long-term productivity of subunit 3.

For sources, Pulliam (1988) predicted that increasing local density would be associated with increasing emigration, as extra individuals should move into sinks in search of mating opportunities. The positive association between increasing local density and emigration for subunit 1 may be due to increased competition for mating opportunities or resources. Similarly, limited mating opportunities may have lead to the positive association between increased resident fertility (i.e., high birth rates in the second year) and emigration from subunit 3. Area 2 may be able to support large population numbers, which may have contributed to the negative association between increasing local density, resident fertility, and emigration for subunit 2.

By the end of 2010, total number of immigrants differed greatly between subunits: subunit 2 had received 3 and 7.5 times higher immigrants compared to subunits 1 and 3, respectively. I do not consider this a border effect, as I did observe individuals moving from subunit 3 to 1. Movement of individuals between subunits can have a profound influence on local population dynamics (Holt 1985, Delibes et al. 2001, Johnson 2004, Zachariah Peery et al.

2006). Immigration is especially important for sink populations where immigrants can balance sink-related losses (Hanski 2001). For example, Robinson et al. (2008) and Cooley et al. (2009) found that compensatory emigration by cougars (*Puma concolor*) from source areas resulted in little to no reduction in local density as individuals were removed from a game management area, which was considered a sink. Here, growth for sink subunit 2 was enhanced by immigration from source subunits 1 and 3. However, immigration into subunits 1 and 3 did not have as large of an influence on growth.

I found evidence of an increasing population trend for subunit 2 in the absence of immigration during the second year, but suggest that realized growth was due to immigration. Therefore, subunit 2 may not actually be a sink, but a 'pseudo-sink' (Watkinson and Sutherland 1995) or an intermediate population (Thomas and Kunin 1999). Watkinson and Sutherland (1995) define 'pseudo-sinks' as populations that are able to function as viable sources, but appear as sinks when immigrants enter causing a density-dependent decrease in reproduction and/or increased mortality. I found no evidence of depressed fertility or negative growth (realized) for subunit 2 in the presence of immigration. Therefore, I do not believe that a pseudo-sink is an appropriate interpretation for the behaviour of subunit 2. A similar pseudo-sink argument could be made for subunit 3, which had low fertility rates when accepting immigrants and high fertility rates when no immigration occurred. Although this is a possibility, it can only be verified with more data about how fertility rates respond to different levels of immigration. For example, if subunit 3 continues to be closed to immigrants and show high fertility rates (i.e., as in year two of my study), then immigrants may depress resident reproduction (i.e., as in the first year of my study). If reliably true, this would suggest that subunit 3 is a pseudo-sink (Watkinson and Sutherland 1995).

For spatially-structured populations, some subunits may be intermediate between sources and sinks, pseudo-sinks, and classical population units (Thomas and Kunin 1999). Thomas and Kunin (1999) propose a 'compensation axis' where the status of each subunit can shift between a true source (i.e., births > deaths; immigration < emigration), a classical or intermediate population (i.e., births = deaths, immigration = emigration), a pseudo-sink (i.e., births < deaths, but births > deaths at low density; immigration > emigration), and a true sink (i.e., births < deaths; immigration > emigration). Position on the compensation axis can change over time depending on environmental and ecological conditions. For example, Johnson (2004) found that

source-sink dynamics in rolled-leaf beetles (*Cephaloleia fenestrata*) existed only after floods caused decreased survival for a flood zone subunit. Migration from upland subunits occurred when mortality was increased due to flooding, but not during non-flood periods. For Sable Island, similar changes of subunit status along a compensation axis may explain long-term spatial heterogeneity in population growth. Continued monitoring of the population under different environmental and ecological conditions (e.g., different subunit densities) will indicate whether subunits are behaving as sources, sinks, or some intermediate.

3.4.3 Subunit-specific demography

I expected that survival rates would show little spatial variation between source and sink subunits, considering that overall age class per captia mortality rates were low during my study (Appendix A, Table A.1.3.2). Alternatively I predicted that emigration and immigration rates would have a large impact on subunit-specific demography. When I considered emigration as death, survival rates for subunits 1 and 3 appeared to be more negatively affected by emigration events compared to subunit 2, which supported my alternative prediction. Doak (1995) used a source-sink model for Yellowstone grizzly bears and demonstrated a similar negative influence of emigration on survival rates of bears in source subunits. Models indicated that increased movement of individuals from good-quality sources into poor-quality sinks reduced population growth for source subunits; here, source related losses were not associated with death, but with emigration.

For source-sink dynamics to be evolutionarily stable there must be re-immigration of individuals from sinks back into sources (Pulliam 1988, Howe et al. 1991). Therefore, residents in sinks must survive to re-immigrate into sources if breeding opportunities become available. Potential re-immigration into sources could explain high survival rates for sink subunit 2 compared to source subunits 1 and 3; although, I did not observe any such re-immigration. Sink subunit 2 may serve as a 'holding area,' where surplus individuals move when breeding opportunities become unavailable in source subunits. Whether or not immigrants breed in sink subunit 2, it may be used as an area in which individuals survive and wait for breeding opportunities to become available in source subunits.

I hypothesized that females would perceive ponds as higher quality relative to water holes; therefore, source subunits would be located in areas with permanent ponds and sinks

would be located in areas with holes. Area 1 contained the highest surface area of ponds and subunit 1 presented as a source. Area 3 contained only holes and, contrary to my prediction, subunit 3 also presented as source. Although, that subunit 1 was found to be the most productive source suggests a trend for source subunits in areas where permanent ponds are located. Subunit 2 had fewer ponds compared to subunit 1, and females used ponds and holes to access water. Subunit 2 was classified as a sink and I found no evidence in support or opposition to my prediction.

I predicted that body condition would be higher from females of source subunits compared to sink subunits. Differences in body condition provided some support for this prediction: body condition for females of subunit 1 was significantly higher compared to females of subunits 2 and 3, but there was no difference in condition between females of subunits 2 and 3. As I did all body condition scoring, observer bias was likely not the cause of these trends. My results suggest that area quality, which may lead to differences in body condition (Rubenstein 1981, Moehlman 1998), is not predicated solely on surface water availability. Rather, area quality may be determined by other factors including forage type and quality. Forage trends are currently being examined with respect to vegetative community-specific browse patterns as a proxy for horse palatability (Tissier 2011, M.Sc. thesis in progress). When such data become available, I believe that incorporation into these methods presented here will enhance our understanding of differences in area-specific (i.e., source-sink) survival and fertility rates.

3.4.4. Influence of immigration on subunit growth

My results suggest that immigration had a considerable influence on subunit-specific growth. High emigration rates from subunits 1 and 3 appeared to augment and enhance growth for sink subunit 2. The relationship between λ_C and λ_M (Zachariah Peery et al. 2006) was useful for assigning source sink status, but only when considered with subunit-specific emigration and immigration rates. For example, subunit 3 showed the most distinctive dynamics compared to subunits 1 and 2. Without considering emigration and immigration rates, in addition to the relationship between λ_C and λ_M, in my opinion, I would have incorrectly assigned sink status to subunit 3 (but see 3.4.2 for explanation for why subunit 3 is not considered the same type of source as subunit 1). If I had not considered subunit-specific emigration and immigration rates

in addition to the relationship between λ_C and λ_M for subunit 3, I would have been unable to determine that growth during the second year occurred in the absence of immigration, but in the presence of emigration.

In Chapter 2.3.4, I suggested that 3-year-old females have the greatest potential to contribute to future population size (i.e., reproductive value) followed by adults. Because immigrants have a positive influence on the size of the subunit into which they move (Howe 1985, Hanski 2001, Johnson 2004, Zachariah Peery et al 2006), sink subunit 2, which was most influenced by immigration, should display higher rates of 3-year-old and adult immigration compared to subunit 1 and subunit 3. Indeed, 3-year-old and adult immigration was highest in subunit 2 compared to subunits 1 and 3. In addition to increasing subunit size themselves, immigrants to sink subunit 2 appeared to continue to contribute to subunit size by reproducing. This trend fits well with Pulliam's (1988) prediction that surplus individuals enter sinks in search of breeding opportunities. Continued monitoring of immigration between and reproductive events within each subunit will provide evidence to verify or refute this trend.

3.4.5 Predictions for future growth trends

The methods I used to assign source-sink status can be used to predict future growth trends for each subunit, but these must be verified with continued monitoring for the possible influence of density dependence. Based on current conditions, source subunit 1 is predicted to maintain an increasing population trend in the presence and absence of immigration. Subunit 3 is predicted to remain stable and perhaps fluctuate around current size in the absence of immigration, but increase in the presence of immigration. As local density increases in source subunits 1 and 3, surplus individuals should emigrate, possibly into sink subunit 2. However, whereas subunit 1 is a consistent producer for the duration of my study, it is unknown how further emigration would impact on subunit 3.

Based on current conditions, sink subunit 2 will continue to have an increasing population trend in the presence of immigration, but may have a decreasing trend in the absence of immigration. Immigrants from source subunits 1 and 3 will continue to augment growth for subunit 2. Therefore, sink subunit 2 is predicted to continue to be a net importer of individuals.

3.4.6 Conclusion

I have provided evidence in support of the contention that spatial heterogeneity influences population growth for the Sable Island horses. The influence of immigration on growth at the subunit-level corresponds to growth at the population-level (Chapter 2). As the presence of a sink can promote a large total population size, especially when adult survival rates in sink areas are high (Howe et al. 1991), it appears that the demographic consequence for sink subunit 2 was to grow by means of immigration into subunit 2 from source subunits 1 and 3.

Table 3.2.1. Criteria used to assign source-sink status to subunits 1, 2, and 3. Interpretation is based on subunit-specific demography, population trends, immigration vs. emigration, realized change in population numbers, and the relationship between changes in local-density and emigration rates.

	Subunit-specific demography	**Population trend** a. Presence of immigration b. Absence of immigration	**Immigration vs. emigration**	**Realized change in population numbers**	**Local-density and emigration rates**
Source	• High and constant survival and fertility • Losses due to emigration have a noticeable effect on survival rates	• Self-sustaining a. Increasing; immigrants have a small effect on subunit growth b. Stable or increasing	• Open or closed to immigrants • Net exporter of individuals • Highest emigration rates • Lowest immigration rates • Emigrants move into sinks	• Increased • Constant increase in population numbers	• Positive association between increasing density and emigration of reproductive aged females
Sink	• Intermediate and variable survival and fertility • Losses due to emigration do not have a noticeable effect on survival rates	• Relies on immigrants for growth a. Stable or increasing; immigrants have a considerable effect on subunit growth b. Decreasing	• Open to immigrants • Net importer of individuals • Lowest emigration rates • Highest immigration rates • Immigrants move from sources	• Increased or decreased • Variable when increasing	• No evidence of a positive association between increasing density and emigration of reproductive aged females

Table 3.3.1.A. Emigration-corrected age class vital rates for subunits 1, 2, and 3 calculated in the absence of immigration from post birth census data (June−September 2008−2010). Fertility rates are calculated at post-birth pulse for 2009 and 2010.

	Survival			**Fertility**		
2008−2009	**Subunit 1**	**Subunit 2**	**Subunit 3**	**Subunit 1**	**Subunit 2**	**Subunit 3**
Foal	0.833 (18)	0.880 (8)	1.000 (11)	-	-	-
Yearling	0.857 (7)	0.750 (4)	1.000 (6)	-	-	-
2-year-old	1.000 (17)	1.000 (9)	1.000 (8)	-	-	-
3-year-old	0.889 (9)	1.000 (5)	1.000 (4)	0.118	0.556	0.125
Adults	0.944 (36)	0.857 (28)	0.950 (20)	0.337	0.153	0.064
2009−2010						
Foal	1.000 (17)	1.000 (11)	1.000 (3)	-	-	-
Yearling	0.929 (14)	0.889 (9)	0.900 (10)	-	-	-
2-year-old	0.833 (6)	1.000 (2)	1.000 (7)	-	-	-
3-year-old	0.944 (18)	0.900 (10)	1.000 (6)	0.167	0	0.429
Adults	0.902 (41)	0.967 (30)	0.870 (23)	0.287	0.376	0.276

Notes: An individual that emigrates from subunit *j* during the pre-birth pulse at $t + 1$ is assumed to have survived in subunit *j* and then emigrated.

Number in parentheses is the number of individuals alive in each subunit at *t*.

Survival rates are calculated for females only; foal survival is a measure of recruitment from *t* for each year.

Table 3.3.1.B. Age class vital rates for resident and immigrant females of subunits 1, 2, and 3 calculated in the presence of immigration from post birth census data (June−September 2008−2010). Survival rates consider emigration events as mortality. Fertility rates are calculated at post-birth pulse (t + 1) for each year.

		Survival			**Fertility**		
	2008−2009	**Subunit 1**	**Subunit 2**	**Subunit 3**	**Subunit 1**	**Subunit 2**	**Subunit 3**
Resident	Foal	0.720 (18)	0.880 (8)	0.910 (11)	-	-	-
	Yearling	0.857 (7)	0.500 (4)	1.000 (6)	-	-	-
	2-year-old	0.941 (17)	1.000 (9)	0.750 (8)	-	-	-
	3-year-old	0.778 (9)	0.800 (5)	0.500 (4)	0.118 [16, 2]	0.556 [9, 5]	0.125 [6, 1]
	Adult	0.917 (36)	0.857 (28)	0.900 (20)	0.337 [40, 15]	0.153 [28, 5]	0.064 [22, 2]
Immigrant	3-year-old	-	-	-	0.500 [2, 1]	0 [1, 0]	0 [0, 0]
	Adult	-	-	-	0 [1, 0]	0 [2, 0]	0 [1, 0]
	2009−2010						
Resident	Foal	0.940 (17)	1.000 (11)	1.000 (3)	-	-	-
	Yearling	0.857 (14)	0.889 (9)	0.800 (10)	-	-	-
	2-year-old	0.833 (6)	1.000 (2)	0.714 (7)	-	-	-
	3-year-old	0.833 (18)	0.900 (10)	0.833 (6)	0.167 [5, 1]	0 [4, 0]	0.429 [5, 3]
	Adult	0.878 (41)	0.933 (30)	0.826 (23)	0.287 [22, 17]	0.376 [37, 15]	0.276 [24, 8]
Immigrant	3-year-old	-	-	-	0 [0, 0]	0.500 [2, 1]	0 [0, 0]
	Adult	-	-	-	0 [1, 0]	0 [5, 0]	0 [0, 0]

Notes: Survival rates consider emigration from a subunit at t + 1 as death.
Number in () is the number of individuals alive in each subunit at t.
Numbers in [] are the number of reproductive-aged females alive in each subunit at t + 1 and the number of post-birth pulse foals those females produced.
Survival rates are calculated for females only; foal survival is a measure of recruitment from t for each year.
Mortalities that may have occurred during or after a migration event but before census at t + 1 are assigned to the survival rate of the subunit from which a migrant originated.

Table 3.3.2. Subunit-specific demographic parameters calculated from annual post-birth pulse censuses (June−September 2008−2010).

	$^{\ddagger}\lambda_C$			$^{\S}\lambda_M$			$^{*}\lambda_C - \lambda_M$			**Δ Total population number**		
	Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3
2008−2009	1.115	1.130	1.000	1.050	0.951	0.932	0.053	0.179	0.068	10	7	0
2009−2010	1.073	1.377	1.041	1.034	1.123	0.999	0.039	0.254	0.041	7	23	2

Notes: $^{\ddagger}\lambda_C$ is the realized rate of population increase calculated from post-birth pulse counts of individuals; λ_C considers all demographic parameters: birth, death, emigration, and immigration.

$^{\S}\lambda_M$ is the estimated rate of population increase calculated from a projection matrix model parameterized with resident survival and fertility rates; λ_M considers emigration as death but does not consider immigration.

$^{*}\lambda_C - \lambda_M$ indicates the influence of immigration on population growth during an annual interval (Zachariah Peery et al. 2006).

Δ Total population number is the total increase in population size including births and immigrants as counted during census at $t + 1$.

Table 3.3.3. Annual and average age class specific immigration and emigration rates for female Sable Island horses among population subunits 1, 2, and 3 observed at post birth censuses (June−September 2008−2010)

			[§]Immigration			[‡]Emigration		
		n	**Subunit 1**	**Subunit 2**	**Subunit 3**	**Subunit 1**	**Subunit 2**	**Subunit 3**
2009	Yearling	33	0.071 (1)	0.222 (2)	0	0.111 (2)	0	0.091 (1)
	2-year-old	15	0	0	0.143 (1)	0	0.250 (1)	0
	3-year-old	34	0.111 (2)	0.100 (1)	0	0.059 (1)	0	0.250 (2)
	Adults	94	0.024 (1)	0.067 (2)	0.044 (1)	0.044 (2)	0.030 (1)	0.036 (1)
	Total		**0.053 (4)**	**0.109 (5)**	**0.046 (2)**	**0.061 (5)**	**0.039 (2)**	**0.082 (4)**
2010	Yearling	31	0	0.083 (1)	0	0.059 (1)	0	0
	2-year-old	30	0	0.200 (2)	0	0.077 (1)	0	0.100 (1)
	3-year-old	14	0	0.500 (2)	0	0	0	0.286 (2)
	Adults	117	0.019 (1)	0.119 (5)	0	0.051 (3)	0.025 (1)	0.069 (2)
	Total		**0.012 (1)**	**0.172 (10)**	**0**	**0.055 (5)**	**0.016 (1)**	**0.114 (5)**
[ϕ]Mean ± SE	Yearling		0.036 ± 0.036 (1)	0.153 ± 0.070 (3)	0	0.085 ± 0.026 (3)	0	0.046 ± 0.046 (1)
	2-year-old		0	0.100 ± 0.100 (2)	0.072 ± 0.072 (1)	0.039 ± 0.039 (1)	0.125 ± 0.125 (1)	0.050 ± 0.050 (1)
	3-year-old		0.056 ± 0.056 (2)	0.300 ± 0.200 (3)	0	0.029 ± 0.029 (1)	0	0.268 ± 0.018 (4)
	Adults		0.022 ± 0.003 (1)	0.093 ± 0.026 (7)	0.022 ± 0.022 (1)	0.048 ± 0.003 (5)	0.028 ± 0.003 (2)	0.052 ± 0.017 (3)
	[x]Total		**0.033 ± 0.021 (5)**	**0.141 ± 0.032 (15)**	**0.023 ± 0.023 (2)**	**0.058 ± 0.003 (10)**	**0.027 ± 0.016 (3)**	**0.098 ± 0.016 (9)**

Notes: [§]Immigration rates are calculated as the proportion of immigrants to the number of residents that survived the current year. [‡]Emigration rates are calculated as the proportion of emigrants to the number of residents that were known to be alive at the end of the previous year. *n* is the total number of females on Sable Island that survived to the end of current year's birth pulse.
[ϕ]Age-class specific means were calculated as the arithmetic mean.
[x]Total mean was calculated by averaging yearly age-class specific immigration or emigration rates and calculating the arithmetic mean from both years.
Immigration and emigration events are assumed to have occurred pre-birth pulse for each year. Numbers in parentheses are total number that moved. Calculations are based on Virgl and Messier 2000.

Table 3.3.4. Behaviour of subunits 1, 2, and 3 showing support for source or sink status. Overall status is based on criteria used to distinguish between sources and sinks (Table 3.2.1).

Criteria	Subunit 1		Subunit 2		Subunit 3	
	Behaviour	**Support**	**Behaviour**	**Support**	**Behaviour**	**Support**
Subunit-specific demography	• High and constant survival and reproduction • Emigration has large effect on survival rates	Source Source	• High and constant survival and reproduction • Emigration has little effect on survival rates	Source Sink	• High and constant survival and reproduction • Emigration has large effect on survival rates	Source Source
Population trend a. Presence of immigration b. Absence of immigration	a. Increasing b. Increasing	Source	a. Increasing b. Increasing and decreasing	Source and sink	a. Increasing b. Decreasing and stable	Source and sink
Immigration vs. emigration	• Open to immigration **Immigrants < Emigrants**	Source	• Open to immigration **Immigrants >> Emigrants**	Sink	• Open and closed to immigration **Immigrants << Emigrants**	Source
Realized change in population numbers	• Constant increase	Source	• Variable increase	Sink	• Constant when increasing	Source
Local-density and emigration rates	As density ↑ emigration rates ↑	Source	As density ↑ emigration rates ↓	Sink	–	–
STATUS	**INCREASING SOURCE**		**INCREASING SINK**		**STABLE SOURCE**	

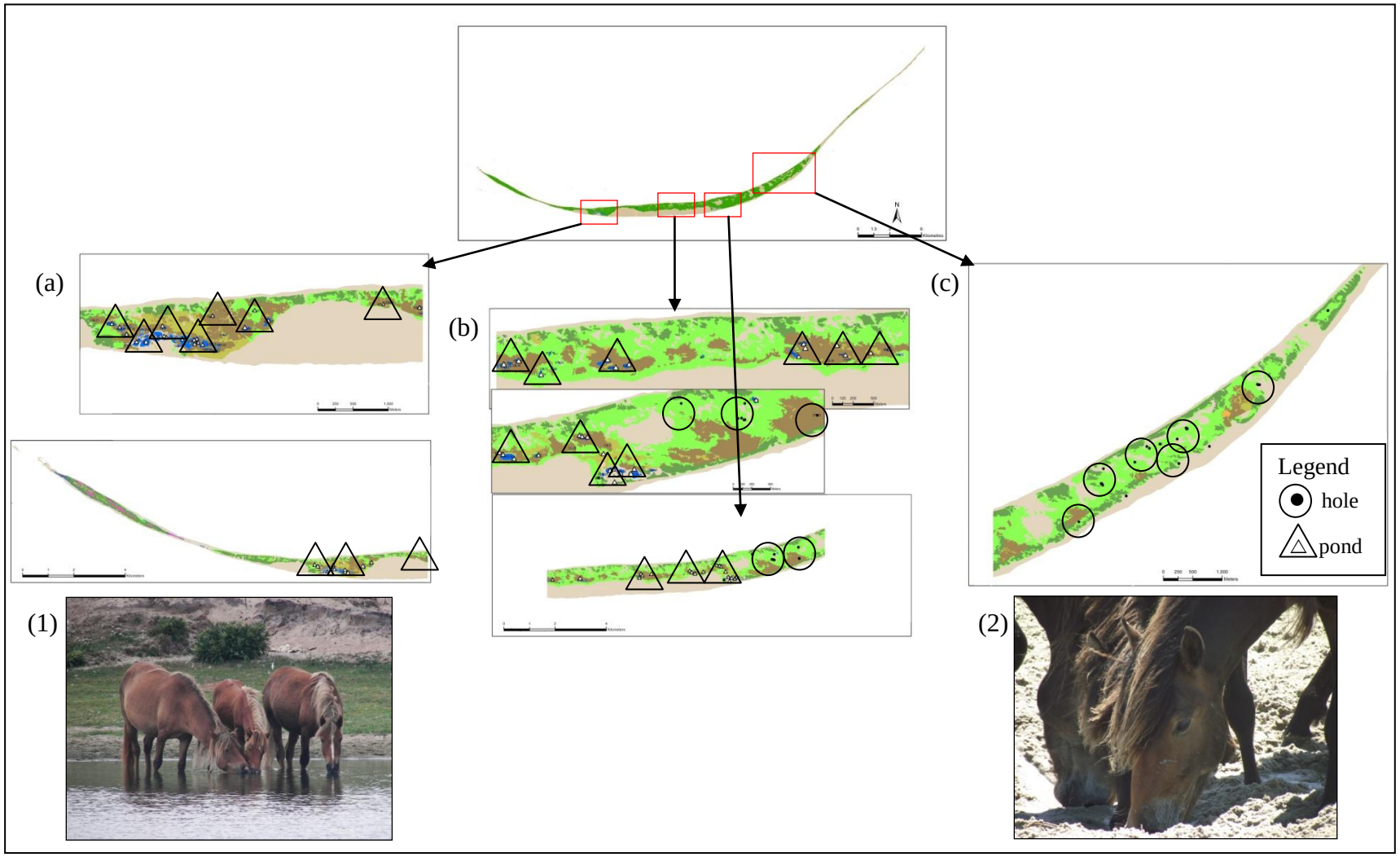

Figure 3.2.1. Availability of water resources to horses on Sable Island along a longitudinal gradient. Circles indicate water holes; triangles indicate permanent water ponds. (a) Most western areas have access to permanent water ponds. (b) Central areas have access to permanent water ponds and holes. (c) Most eastern areas have access to holes only. (1) Horses using permanent water ponds; (2) horses using water holes. Maps credits: A. Muise (2011); photograph credit: A. Contasti (2010).

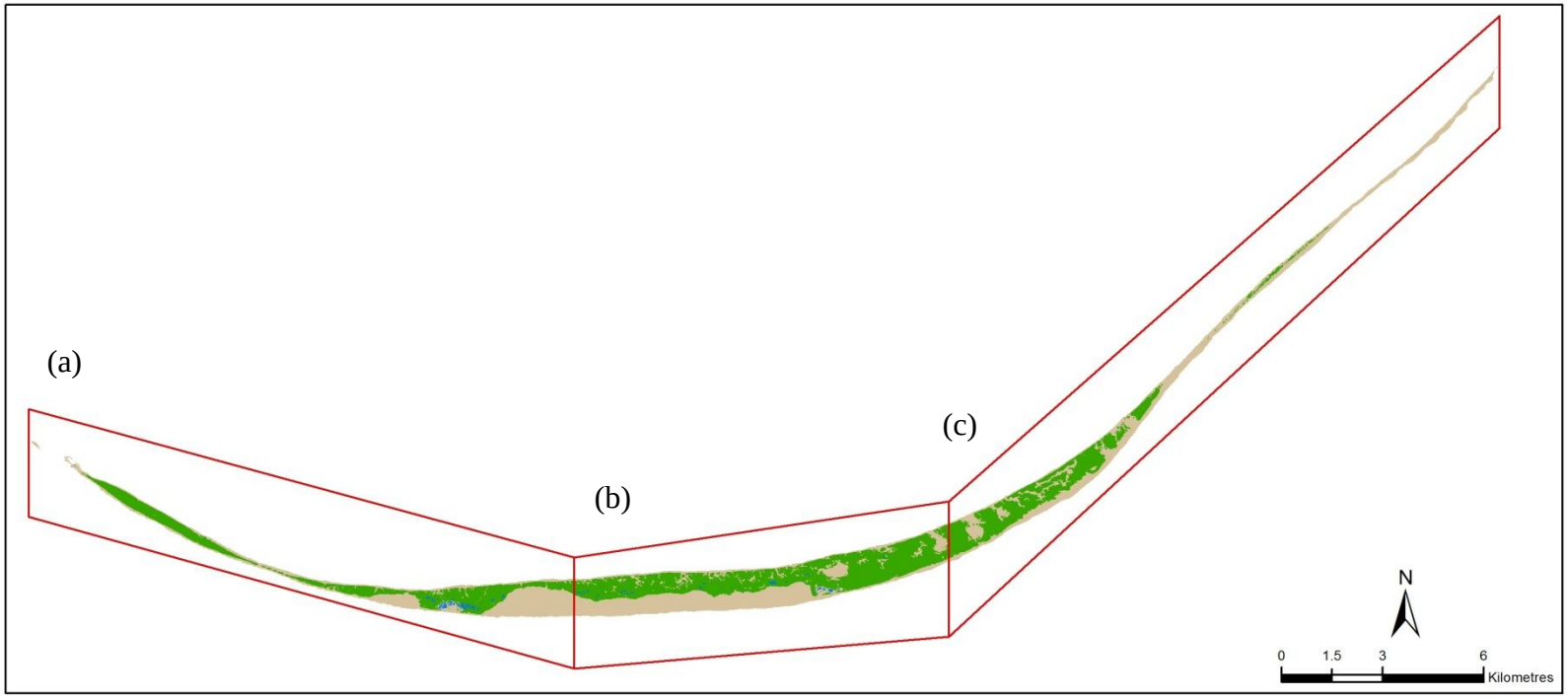

Figure 3.3.1. Map of Sable Island showing three neighbouring island area divisions based on spatial distribution of water resources and female positioning. Spatial population substructure indicated three subunits; area boundaries define spatial use of one subunit (a) Area 1, most western (7.891 km^2; water ponds 0.122 km^2), (b) Area 2, central (13.260 km^2; water ponds 0.096 km^2 and dug holes), (c) Area 3, most eastern (8.786 km^2, dug holes only). Map is from A. Muise (2011).

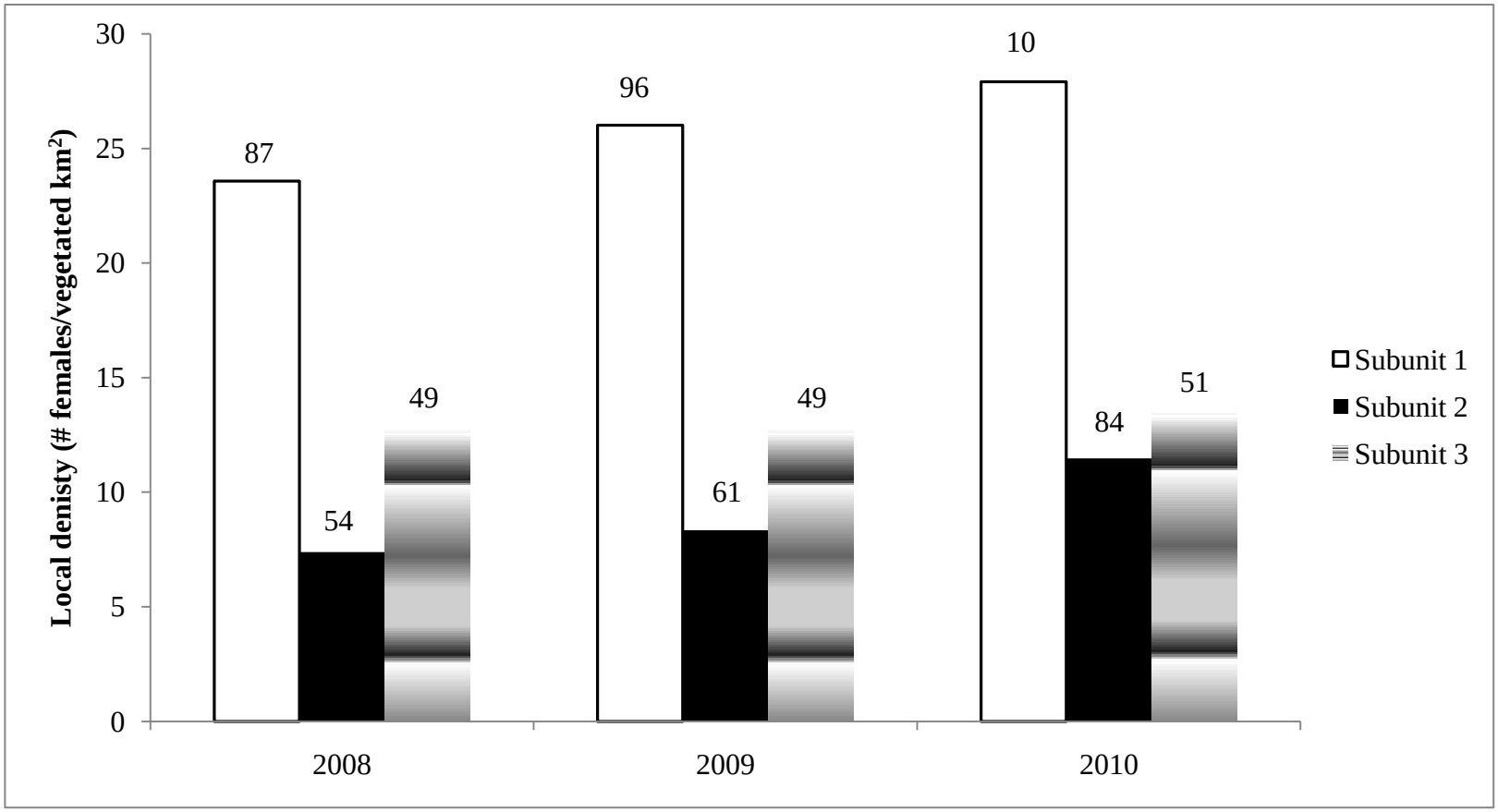

Figure 3.3.2. Change in local density (total number of females/vegetated km^2) of subunits 1, 2, and 3 over the study period (2008−2010). Total vegetated surface area for each subunit are: subunit 1 (Area 1): 3.69 km^2; subunit 2 (Area 2): 7.32 km^2; subunit 3 (Area 3): 3.87 km^2. Number above bar is total number of females alive at the end of year for each subunit.

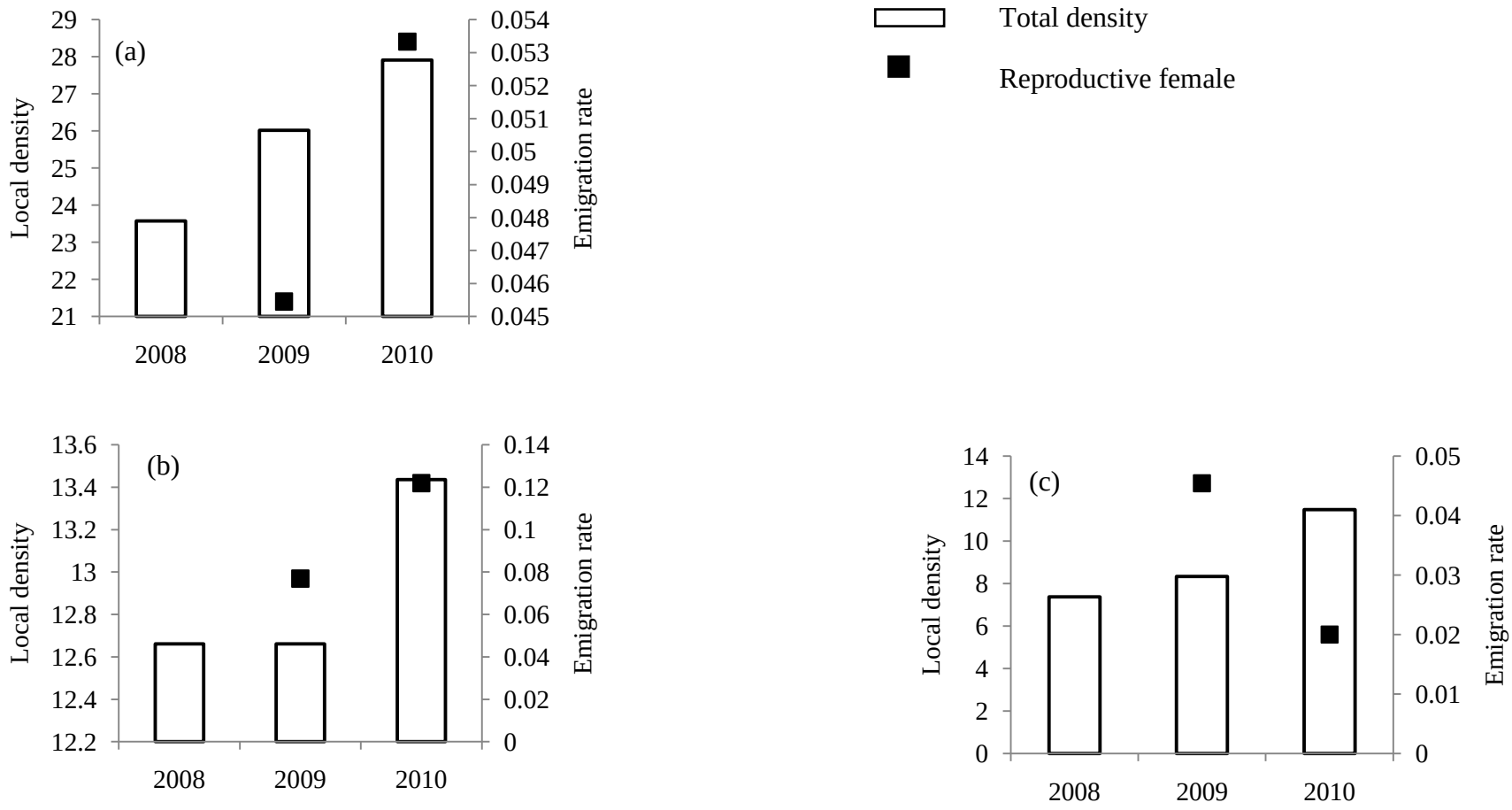

Figure 3.3.3. Change in total density (# females/vegetated km^2) of female horses using areas 1 (a), 3 (b), and 2 (c) over study period (2008−2010) and associated pre-birth pulse (2009, 2010) emigration rates of reproductive females.

CHAPTER 4: GENERAL DISCUSSION

4.1 THESIS OVERVIEW

The population of horses on Sable Island grew from 390 to 484 horses between 2008 and 2010. I monitored individuals for two consecutive animal years (1 August−31 July the following year) and collected data on survival, reproduction, and movement data for known females (98.7% of all females). Annual population growth was investigated using matrix population models (Caswell 2001); I identified source-sink dynamics (Pulliam 1988, Virgl and Messier 2000, Zachariah Peery et al. 2006) as an explanation for spatial heterogeneity in population-level growth.

My main objectives were to:

(1) Provide an explanation for the basis of population dynamics by estimating: (i) λ, (ii) stable age distribution, and (iii) age class reproductive values. I determined: (iv) how future λ would respond to proportional changes in each vital rate by estimating elasticity values, and (v) the contribution that realized variation in vital rates made to annual variation in λ.

(2) Identify spatially distinct subunits in the population and compare: (i) demographic and growth trends in the presence and absence of immigration, (ii) immigration and emigration rates, and (iii) the relationship between changes in local density, increased fertility, and reproductive aged emigration rates. I wanted to determine if source-sink dynamics could provide an explanation for population-level growth.

My main conclusions are:

(1) The population increased in size during both years, however at a more rapid rate during the second year. The population appears to have converged to its stable age distribution, suggesting current λ has been sustained for some time. Three-year-olds and adults were the only females to produce foals, and these females made the greatest contribution to future population size. Future growth is predicted to be most influenced by proportional changes in adult survival. However, annual variation in λ between 2008 and 2010 was attributed to increased adult fertility and foal survival during the second year.

(2) The population can be stratified into three spatially distinct subunits with differing access to a gradient of water resources. Source-sink dynamics appears to be driving current spatial heterogeneity in population-level growth. Subunit source-sink status was most influenced by emigration and immigration; subunits 1 and 3 were classified as sources

and subunit 2 was identified as a sink. Evidence suggests that continued growth of the total population is made possible by individual emigration from more productive subunits into less productive ones. The most productive source was in the west of the island where permanent ponds are located.

4.2 COMMENTARY

Yearly variation in adult fertility and foal survival appears to have made the largest contribution to current temporal variation in λ; however, annual growth may also have resulted from high survival and fertility rates for all age classes. I did not collect annual environmental data and so could not determine the underlying factors influencing current vital rates, but it is likely that environmental factors (e.g., mild winters or high forage availability) and demographic stochasticity influenced vital rates during my study. My results suggest that current population growth is a consequence of internal source-sink dynamics, which has lead to spatial heterogeneity in population-level growth.

4.2.1 Population prospective

Future λ is predicted to be most greatly influenced by proportional changes in adult survival. Therefore, I expect that current λ will decline the most when adult female survival declines. However, as adult female survival in many ungulates remains relatively constant over time (e.g., Galliard et al. 2000 for review), it is possible that temporal variation in λ for the Sable Island horses may continue to be controlled by variation in vital rates associated with early life (i.e., juvenile survival and 3-year-old and adult fertility). Although my results suggest that current λ has been sustained for some time, no population grows *ad infinitum*, and thus λ must decline in the future.

Spatial heterogeneity in population-level growth appeared to be most influenced by movements between subunits. My assessment of source-sink status suggests that subunit 1 will remain as an increasing source in the presence and absence of immigration; subunit 3 will remain as a stable source in the absence of immigration, but an increasing source in the presence of immigration. As local density increases in subunits 1 and 3, surplus individuals emigrate into sink subunit 2 where they augment local-population growth; thus, total population size may

remain high. However, whereas subunit 1 has proven to be a consistent producer, it is unknown how further emigration would impact subunit 3. Subunit 2 should remain as a sink; however, if current population-level λ continues to be sustained, it may be possible for sink subunit 2 to eventually become a source as more individuals immigrate from source subunits 1 and 3 (Howe et al. 1991, Watkinson and Sutherland 1995, Thomas and Kunin 1999). Confirmation of these predictions can only be made with continued monitoring of the population.

4.2.2 Management implications

On 18 May 2010, the Governments of Canada and Nova Scotia announced plans to possibly work toward designating Sable Island as a National Park under the National Parks Act. My results may serve as a baseline for monitoring research by the Parks Canada Agency for managing Sable Island and its wildlife. For example, I was able to identify areas of sources and sinks on Sable Island for the horses, which managers may find useful for future monitoring. That these areas relate to water availability may also be of interest. More in-depth analyses of population dynamics will require further research, as suggested below.

4.2.3 Recommendations for future research

My results were drawn from two animal years of survival, fertility, and movement data collected from the female portion of the population only. Although I provide an explanation for population dynamics in relation to current environmental conditions, I was unable to address several questions (see below for examples) that need to be answered with continued monitoring. I would recommend that the following research initiatives be implemented:

(1) Continued monitoring of the entire population using island-wide census methods. Additional years of census data will allow research to incorporate factors such as density dependence and environmental stochasticity, which are known to regulate λ in other free-ranging ungulate populations (for review see: Sæther 1997, Gaillard et al. 2000, and Clutton-Brock and Coulson 2002).

(2) Continued monitoring of subunit-specific demography and movement between subunits to verify source-sink status. Additional years of monitoring data may eventually lead to

uncovering the proximate and ultimate causes of internal source-sink dynamics. See (5) for recommendation regarding male horses and source-sink dynamics.

(3) Population censuses during additional seasons: (i) pre- to mid-birth pulse to monitor early deaths of foals and correct biases in fertility estimates, (ii) winter to quantify mortality, spacing behaviours, and possible movement between subunits.

(4) Measure trait variation between individuals and include comparisons in demographic and source-sink analyses (e.g., compare traits between non-dispersers and dispersers). For example, determine body condition using a method that measures weight or skeletal size (i.e., hind leg length; see: Pelletier et al. 2007) or assign reproductive condition relating to previous year's reproductive events.

(5) Incorporate males into analyses. A recent review of the dynamics of ungulate populations (see Mysterud et al. 2002) has suggested that males may play an important role in population dynamics. To incorporate males into demographic analyses, paternity data must be obtained. Monitoring of male movements may be an important aspect of source-sink dynamics as it is possible that males move between subunits more frequently than females.

(6) Establish quality of vegetative communities as forage resources for horses. Incorporate forage quality into area divisions to verify habitat quality for each subunit. Formulate habitat-selection functions for residents and emigrants/immigrants to analyze movements. In addition, collect annual environmental variables to include in analyses (e.g., temperature and precipitation).

4.3 FINAL REMARKS

I studied the dynamics of a natural population at a scale between the individual- and population-level. My results are unique given that I was able to monitor life history events and movement between different areas for almost every female in the population. Therefore, the approach I used may be considered a first step toward understanding the influence of area-specific demography on population-level growth, and as a hypothesis for the direct demographic consequences of internal source-sink dynamics.

LITERATURE CITED

Amarasekare, P. 1994. Spatial population structure in the banner-tailed kangaroo rat, *Dipodomys spectabilis*. Oecologia **100**:166–176.

Albon, S. D., T. N. Coulson, D. Brown, F. E. Guinness, J.M. Pemberton, and T.H. Clutton-Brock. 2000. Temporal changes in key factors and key age groups influencing the population dynamics of female red deer. Journal of Animal Ecology **69**:1099–1110.

Applied Geomatics Research Group (AGRG). 2011. Sable Island, Nova Scotia 2009 topography and land cover atlas. Middleton, Nova Scotia, pp. 122.

Armstrong, B. 1981. Sable Island. Doubleday Canada Limited, Toronto, Canada.

Berger, J. 1986. Wild Horses of the Great Basin. University of Chicago Press, Chicago.

Beson, K. 1998. Towards a conservation strategy for Sable Island. Environment Canada, Canadian Wildlife Service, Atlantic Region.

Bonenfant, C., J.-M. Gaillard, F. Klein, and J.-L. Hamann. Can we use the young : female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. Journal of Applied Ecology **42**:361−370.

Boyd, L. & R. Keiper. (2005) Behavioural ecology of feral horses. Pages 55−82 *in*: The Domestic Horse: The Origins, Development, and Management of its Behaviour. D. S. Mills and S. M. McDonnell, editors. Cambridge University Press, Cambridge, UK.

Brault, S. and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). Ecology **74**:1444−1454.

Bui, R., R. N. Buliung, and T. K. Remmel. 2010. aspace: a collection of functions for estimating centrographic statistics and computational geometries for spatial point patterns. R package version 2.5. http://CRAN.R-project.org/package=aspace.

Cameron, E. Z., W. L. Linklater, K. J. Stafford and C. J. Veltman. 1999. Birth sex ratios relate to mare condition at conception in Kaimanawa horses. Behavioural Ecology **10**:472–475.

Cameron, E. Z. and W. L. Linklater. 2007. Extreme sex ratio variation in relation to change in condition around conception. Biology Letters **3**:395−397.

Carroll, C. L. and P. J. Huntington. 1988. Body condition scoring and weight estimation of horses. Equine Veterinary Journal **20**:41–45.

Caswell, H. 1996. Analysis of life table response experiments II. Alternative parameterization for size- and stage-structured models. Ecological Modelling **88**:73–82.

Caswell, H. 1997. Methods of matrix population analyses. Pages 19–58 *in* S. Tuljapurkar and H. Caswell, editors. Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York, New York, USA.

Caswell, H. 2001. Matrix population models construction, analysis, and interpretation. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.

Catling, P. M., B. Freedman and Z. Lucas. 1984. The vegetation and phytogeography of Sable Island, Nova Scotia. Proceedings of the Nova Scotia Institute of Science **34**:181−247.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley-Interscience, New York, USA.

Chamaillé-Jammes, S., M. Valeix, and H. Fritz. 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. Journal of Applied Ecology **44**:625–633.

Christie, B. J. 1995. The Horses of Sable Island. Pottersfield Press, Nova Scotia, Canada.

Clutton-Brock, T. H. and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London B **357**:1285−1298.

Coltman, D.W., W.D. Bowen & J.M. Wright. (1998) Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites. Proceedings of the Royal Society of London B **265**:803−809.
Cooley, H. S., R. B. Wielgus, G. Koehler, and B. Maletzke. 2009. Source populations in carnivore management: cougar demography and emigration in a lightly hunted population. Animal Conservation **12**:321−328.
Coulson, T., S. Albon, F. Guinness, J. Pemberton and T. Clutton-Brock. 1997 Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus).* Ecology **78**:852–863.
Coulson, T., F. Guinness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. Ecology **85**:411−422.
Coulson, T., J.-M. Gaillard, and M. Festa-Bianchet. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology **74**:789–801.
Coulson, T., T. G. Benton, P. Lundberg, S. R. X. Dall, B. E. Kendall and J.-M. Gillard. 2006 Estimating individual contributions to population growth: evolutionary fitness in ecological time. Proceedings of the Royal Society B **273**:547–555.
Cronin, J. T., K. J. Haynes, and F. Dillemuth. 2004. Spider effects on planthopper mortality, dispersal, and spatial population dynamics. Ecology **85**:2134–2143.
Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412−1423
Davies, N.B. 1991. Mating systems. Pages 263−300 *in* J. R. Krebs and N. B. Davies, editors. Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific Publications, Oxford.
Davies Morel, M. C. G. 2008. Equine Reproductive Physiology, Breeding and Stud Management. 3rd Edition. CABI, UK.
Delibes, M., P. Gaona, and P. Ferreras. 2001. Effects of an attractive sink leading into maladaptive habitat selection. The American Naturalist **158**:279–285.
de Villers, M. and S. Hirtle. 2004. Sable Island: The Strange Origins and the Curious History of a Dune Adrift in the Atlantic. Walker & Company, New York, USA.
Dixon, P., N. Friday, P. Ang, S. Heppell, and M. Kshatriya. 1997. Sensitivity analysis of structured-population models for management and conservation. Pages 471−514 *in* Structured-Population Models is Marine, Terrestrial, and Freshwater Systems. Tuljapurkar, S. and H. Caswell. pp. Chapman & Hall, New York, New York, USA.
Doak, D. F. 1995. Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone grizzly. Conservation Biology **9**:1370−1379.
Environment Canada. 2011. National Climate Data and Information Archive. www.climate.weatheroffice.ec.gc.ca
Feh, C. 2005. Relationships and communication in socially natural horse herds. Pages 83-93 *in* The Domestic Horse: The Origins, Development, and Management of its Behaviour. D. S. Mills and S. M. McDonnell. Cambridge University Press, Cambridge, UK.
Foppen, R. P. B., J. P. Chardon, and W. Liefveld. 2000. Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. Conservation Biology **14**:1881–1892.

Forchhammer, M.C., T.H. Clutton-Brock, J. Lindström & S.D. Albon. (2001) Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology **70**:721–729.

Fretwell, S. D. and H. L. Lucas. 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheroretica **19**:16–36.

Gaillard, J.-M., M. Festa-Bianchet and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. TREE **13**:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367–393.

Gaillard, J.-M., M. Hebblewhite, A. Loison, M. Fuller, R. Powell, A. Basille, and B. Van Moorter. Habitat-performance relationships: finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society B **365**: 2255–2265.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology **81**: 33−45.

Guinness, F.E., T.H. Clutton-Brock & S.D. Albon. (1978) Factors affecting calf mortality in red deer (*Cervus elaphus)*. *Journal of Animal Ecology*, **47(3)**, 817-832.

Hanski, I. 2001. Population dynamic consequences of dispersal in local populations and metapopulations. Pages 283–298 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Osford University Press, New York, New York, USA.

Harris, N. C., M. J. Kauffman, and L. S. Mills. 2008. Inferences about ungulate population dynamics derived from age ratios. Journal of Wildlife Management **72**:1143−1151.

Heitor, F., M. do Mar Oom and L. Vicente. 2006. Social relationships in a heard of Sorraia horses Part II. Factors affecting affiliative relationships and sexual behaviours. Behavioural Processes **73**:231−239.

Hewison, J. M., J.-M. Gaillard, P. Kjellander, C. Toïgo, O. Liberg and D. Delorme. 2005. Big mothers invest more in daughters – reversed sex allocation in a weakly polygynous mammal. Ecology Letters **8**:430-437.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology **28**:181–208.

Horvitz, C., D. W. Schemske, and H. Caswell. 1997. The relative "importance" of life-history stages to population growth: prospective and retrospective analyses. Pages 247–271 *in* S. Tuljapurkar and H.Caswell, editors. Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York, New York, USA.

Howe, R. W., G. J. Davis, and V. Mosca. 1991. The demographic significance of 'sink' populations. Biological Conservation **57**:239–255.

Iverson, S. A. and D. Esler. 2010. Harlequin duck population injury and recovery dynamics following the 1989 *Exxon Valdez* oil spill. Ecological Applications **20**:1993–2006.

Jacobson, A. R., A. Provenzale, A. von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004. Climate forcing and density dependence in a mountain ungulate population. Ecology **85**:1598−1610.

Johnson, D. M. 2004. Source-sink dynamics in a temporally heterogeneous environment. Ecology **85**:2037–2045.

Johnson, H. E., L. S. Mills, T. R. Stephenson, and J. D. Wehausen. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications **20**:1753–1765.
Kalisz, S. and M. A. McPeek. 1993. Demography of an age-structured annual: resampled projection matrices, elasticity analysis, and seed band effects. Ecology **73**:1082–1093.
Keiper, R. and K. Houpt. 1984. Reproduction in feral horses: an eight-year study. American Journal of Veternary Research **45**:991–995.
Kenkel, N. C. 2006. On selecting an appropriate multivatriate analysis. Canadian Journal of Plant Science **86**:663−667.
Kreuzer, M. P. and N. J. Huntly. 2003. Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. Oecologia **134**:343–349.
Ladewig, J., E. Søndergaard and J. W. Christensen. 2005. Ontogeny: preparing the young horse for its adult life. Pages 139–149 *in* The Domestic Horse: The Origins, Development, and Management of its Behaviour. D. S. Mills and S. M. McDonnell. Cambridge University Press, Cambridge., UK.
Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology **63**:607–615.
Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics **21**:1−18.
Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika **33**: 183−212.
Linklater, W. L. 2000. Adaptive explanation in socio-ecology: lessons from the equidae. Biological Review **75**:1–20.
Linklater, W. L., E. Z. Cameron, K. J. Stafford and C. J. Veltman. (2000) Social and spatial structure and range use by Kaimanawa wild horses (*Equus caballus:* Equidae). New Zealand Journal of Ecology **24**:139−152.
Lloyd, P. H. and O. A. E. Rasa. 1989. Status, reproductive success and fitness in Cape Mountain zebra (*Equus zebra zebra*). Behavioural Ecology and Sociobiology **25**:411−420.
Lucas, Z. L., P. D. McLoughlin, D. W. Coltman and C. Barber. 2009. Multiscale analysis reveals restricted gene flow and a linear gradient in heterozygosity for an island population of feral horses. Canadian Journal of Zoology **87**:1−7.
Manley, B. F. J. 1998. Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapman and Hall, London, UK. pp. 34–68.
Marshal, J. P., V. C. Bleich, P. R. Krausman, M. L. Reed, and N. G. Andrew. 2006. Factors affecting habitat use and distribution of desert mule deer in an arid environment. Wildlife Society Bulletin **34**:609–619.
Marshall, A. J. 2009. Are montane forests demographic sinks for Bornean white-bearded gibbons *Hylobates albibarbis?* Biotropica **41**:257–267.
Mauritzen, M., A. E. Derocher, Ø. Wiig, S. E. Belikov, A. N. Boltunov, E. Hansen, and G. W. Garner. 2002. Using satellite telemetry to define spatial population structure in polar bears in the Norwegian and western Russian Arctic. Journal of Applied Ecology **39**:79–90.
Mayberry, R. J. and E. Elle. 2010. Conservation of a rare plant requires different methods in different habitats: demographic lessons from *Actaea elata*. Oecologia **164**:1121–1130.
Mayer, C., K. Schieg, and G. Pasinelli. 2009. Patchy population structure in short-distance migrant: evidence from genetic and demographic data. Molecular Ecology **18**:2353–2364.

McCort, W. D. 1984. Behavior of feral horses and ponies. Journal of Animal Science **58**:493–499.
McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon, USA.
McGreevy, P. 2004. Equine Behaviour: A Guide for Veterinarians and Equine Scientists. Saunders, London, UK.
McLoughlin, P. D., J. D. Dunford and S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. Journal of Animal Ecology **74**:701−707.
McLoughlin, P. D., M. S. Boyce and T. Coulson. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society of London B **273**:1449−1454.
McLoughlin, P. D., J.-M. Gaillard and M. Boyce. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology **88**:3192−3201.
McLoughlin, P. D., T. Coulson and T. Clutton-Brock. 2008. Cross-generational effects of habitat and density on life history in red deer. Ecology **89**:3317−3326.
McPeek, M. A. and S. Kalisz. 1993. Population sampling and bootstrapping in complex designs: demographic analysis. *in*: Design and Analysis of Ecological Experiements**.** S. M. Scheiner and J. Gurevitch, editors. Chapman and Hall, New York, New York, USA. pp. 232–252.
Mobæk, R. A. Mysterud, L. E. Loe, Ø. Holand, and G. Austrheim. 2009. Density dependent and temporal variability in habitat selection by a large herbivore: an experimental approach. Oikos 118: 209–218.
Moehlam, P. D. 1998. Feral asses (*Equus africanus*): intraspecific variation in social organization in arid and mesic habitats. Applied Animal Behaviour Science **60**:171–195.
Monard, A.-M., P. Duncan, H. Fritz & C. Feh. 1997. Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. Behavioural Ecology and Sociobiology **41**:243–249.
Morris, W. F. and D. F. Doak. 2002. Quantitative Conservation Biology theory and practice of population viability analysis. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.
Mysterud, A., T. Coulson, and N. C. Stenseth. 2002. The role of males in the dynamics of ungulate populations. Journal of Animal Ecology **71**:907−915.
Naranjo, E. J. and R. E. Bodmer. 2007. Source-sink systems and conservation of hunted ungulates in the Lacandon Forest, Mexico. Biological Conservation **138**:412–420.
National Museum of Natural Sciences Canada. 1970. Fauna of Sable Island and its Zoogeographic Affinities: a Compendium.
Neubert, M. G. and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology **81**:1613−1628.
Patterson, G. 1894. Sable Island: its history and phenomena. Transactions of the Royal Society of Canada **2**:3−48.
Pease, C. M. and D. J. Mattson. 1999. Demography of the Yellowstone grizzly bears. Ecology **80**:957−975.
Pelletier, F., T. Clutton-Brock, J. Pemberton, S. Tuljapukar, and T. Coulson. 2007. The evolutionary demography of ecological change: linking trait variation and population growth. Science **315**:1571–1574.
Peterson, R. O., R. E. Page, and K. M. Dodge. 1984. Wolves, moose, and the allometry of population cycles. Science **224**:1350−1352.

Picard, N., P. Chagneau, F. Mortier, and A. Bar-Hen. 2009. Finding confidence limits on population growth rates: Bootstrap and analytic methods. Mathematical Biosciences **219**:23–31.

Plante, Y., J. L. Vega-Pla, Z. Lucas, D. Colling, B. de March and F. Buchanan. 2007. Genetic diversity in a feral horse population from Sable Island, Canada. Journal of Heredity, **98**:594–602.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist **132**: 652–661.

Pulliam, H. R., J. B. Dunning, Jr., and J. Liu. 1992. Population dynamics in complex landscapes: a case study. Ecological Applications **2**:165–177.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management **71**:795–803.

Ritter, R. C. and Bednekoff, P. A. Dry season water, female movements and male territoriality in springbok: preliminary evidence of waterhole-directed sexual selection. African Journal of Ecology **33**:395–404.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications **18**:1028–1037.

Rubenstein, D. I. 1981. Behavioural ecology of island feral horses. Equine Veterinary Journal **13**:27–34.

Rubenstein, D.I. 1994. The ecology of female social behaviour. Pages 13−28 *in*: P. J. Jarman and A. Rossiter, editors. Animal Societies, Individuals, Interactions, and Organization. Horses, Zebras, and Asses. Kyoto University Press, Kyoto, Japan.

Rutberg, A. T. and R. R. Keiper. 1993. Proximate causes of natal dispersal in feral ponies: some sex differences. Animal Behaviour **46**:969−975.

Sæther, B.-E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. TREE **12**:143–149.

Sæther, B.-E. And Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**: 642–653.

Salter, R. E. and R. J. Hudson. 1982. Social organization of feral horses in western Canada. Applied Animal Ethology **8**:207−223.

Saltz, D. and D. I. Rubenstein. 1995. Population dynamics of a reintroduced Asiatic wild ass (*Equus hemionus)* herd. *Ecological Applications* **5**:327−335.

Sanz, J. J. 1998. Effects of geographic location and habitat on breeding parameters of Great Tits. The Auk **115**:1034–1051.

Siegel, S. and N. J. Castellan, Jr. 1988. Nonparametric statistics for the behavioural sciences. McGraw Hill, Inc. New York, New York, USA.

Stubben, C. J. and B. G. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software **22**:1–23.

Sutherland, W. J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford, UK.

Thomas, C. D. and W. E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology **68**:647–657.
Tissier, E.J. 2011. M.Sc. Thesis, University of Saskatchewan, Saskatoon, Canada
van Sickle, J. 1997. Using mean similarity dendrograms to evaluate classifications. Journal of Agricultural, Biological, and Environmental Statistics **2**:370−388.
van Tienderen, P. H. 2000. Elasticities and the link between demographic and evolutionary dynamics. Ecology **81**:666–679.
Venables, W. N. & Ripley, B. D. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York, USA.
Virgl, J. A. and F. Messier. 2000. Assessment of source-sink theory for predicting demographic rates among habitats that exhibit temporal changes in quality. Canadian Journal of Zoology **78**:1483–1493.
Watkinson, A. R. and W. J. Sutherland. 1999. Sources, sinks and pseudo-sinks. Journal of Animal Ecology **64**:126–130.
Welsh, D.A. 1975 Population, behavioural, and grazing ecology of the horses of Sable Island, Nova Scotia. Ph.D. Thesis, Dalhousie University, Nova Scotia, 402 pp.
Zachariah Peery, M., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. Ecological Applications **16**:1516–1528.
Zeigler, S. L., W. F. Fagan, R. DeFries, and B. E. Raboy. 2010. Identifying important forest patches for the long-term permisstence of the endangered gold-headed lion tamarin (*Leontopithecus chrysomelas*). Tropical Conservation Science **3**:63−77.

APPENDIX A: INTRODUCTION TO SABLE ISLAND FERAL HORSES

Table A.1.3.1. Changes in post-birth pulse population size for the Sable Island feral horses between 2008 and 2010. Annual post-birth pulse population sizes are given by age class and sex.

	Total	Foals	Yearlings	Young	Adults
2008	**390**	**76**	**32**	**124**	**158**
Males	200	39	16	71	74
Females	190	37	16	53	84
2009	**442**	**80**	**69**	**121**	**172**
Males	237	51	36	72	78
Females	205	29	33	49	94
2010	**484**	**82**	**73**	**120**	**209**
Males	247	37	44	65	101
Females	237	45	29	55	108

Table A.1.3.2. Age class specific mortality and survival rates for male and female Sable Island feral horses for winter seasons between 2008 and 2010.

		2008−2009		2009−2010	
	Age class	Mortality rate	Survival rate	Mortality rate	Survival rate
Males	Foal	0.088	0.912	0.135	0.865
	Yearling	0	1.000	0.139	0.861
	Young	0.070	0.930	0.069	0.931
	Adult	0.070	0.930	0.141	0.859
Females	Foal	0.088	0.912	0	1.000
	Yearling	0.125	0.875	0.091	0.909
	Young	0.019	0.981	0.061	0.939
	Adult	0.088	0.913	0.074	0.926

Notes: Winter season mortality and survival were defined as events which occurred outside of my field season (i.e., post-birth pulse summer season).
Mortality was assigned to an individual not observed in consecutive seasons
Foal survival does not consider deaths which occurred before the post-birth pulse season (i.e., first few weeks after parturition)

Table A.1.3.3. Annual age class, post-birth pulse sex ratios for Sable Island feral horses during 2008, 2009, and 2010. Sex ratios are given as number of males to one female.

	Total	Foals	Yearlings	Young	Adults
2008‡	**390**	**76**	**32**	**124**	**158**
Males	1.05	1.05	1	1.34	0.88
Females	1	1	1	1	1
2009‡	**442**	**80**	**69**	**121**	**172**
Males	1.16	1.76*	1.09	1.47*	0.83
Females	1	1	1	1	1
2010‡	**484**	**82**	**73**	**120**	**209**
Males	1.04	0.82	1.52	1.18	0.94
Females	1	1	1	1	1
Average	1.08	1.21	1.20	1.33	0.88
	1	1	1	1	1

Notes: *Indicates sex ratio significantly different from parity (foals: $P = 0.018$; young: $P = 0.045$)

Foal sex ratios do not consider only those individuals surviving to the post-birth pulse

‡Numbers in bold are total population numbers at end birth-pulse in each age class for a given year; see Table A.1.3.1 for total number of males and females in each age class.

Table A.1.3.4. Size and composition of family bands on Sable Island during 2008, 2009, and 2010

			Foals		Yearlings		Young		Adults	
		Band Size	Female	Male	Female	Male	Female	Male	Female	Male
2008	Min	2	0	0	0	0	0	0	0	0
	Max	15	2	2	1	1	4	6	5	3
	Average ± SD	6.59 ± 2.91	0.65 ± 0.74	0.65 ± 0.66	0.33 ± 0.45	0.29 ± 0.46	1.08 ± 1.11	0.84 ± 1.17	1.57 ± 1.06	1.18 ± 0.56
2009	Min	2	0	0	0	0	0	0	0	0
	Max	13	2	3	2	3	3	4	5	3
	Average ± SD	6.63 ± 2.64	0.43 ± 0.63	0.64 ± 0.84	0.59 ± 0.63	0.75 ± 0.74	0.88 ± 0.94	0.48 ± 0.83	1.77 ± 1.10	1.09 0.48
2010	Min	2	0	0	0	0	0	0	0	0
	Max	15	3	4	4	4	4	4	4	3
	Average ± SD	6.14 ± 2.74	0.59 ± 0.71	0.64 ± 0.87	0.61 ± 0.86	0.77 ± 1.07	0.74 ± 0.77	0.59 ± 0.83	1.09 ± 0.70	1.11 ± 0.53

Table A.1.3.5. Structure and dynamics of family bands on Sable Island during 2008, 2009, and 2010. Bands are defined by band stallions. Structure is described as single stallion and multi-male bands. Dynamics are described as band formation and collapse within (i.e., summer season) and between (i.e., winter season) years.

		2008	2009	2010
	Total bands	**51**	**56**	**70**
Structure	Total SS[♦]	32	45	57
	Total MM[§]	19	11	13
Dynamics	[♁]Total new	-	17	32
	[♦]Total collapsed *t*	0	2	3
	[○]Total collapsed *t* + 1	10	3	-

Notes: [♦]SS: Single stallion bands; family bands with one band stallion

[§]MM: Multi-male bands; family bands with one band stallion and additional adult males. Bands had two or three adult males

[♁]Total new gives the number of bands at *t* + 1 which were not observed during the previous year's census at *t*. Formation indicates a band stallion that had acquired more than three new members to his band from the previous year or a band stallion that was not in possession of a band during the previous year.

[♦]Total collapsed at *t* gives the number of bands that collapsed during summer field seasons at *t*. Collapse indicates a band stallion that lost his band to another adult male.

[○]Total collapse at *t* + 1 gives the number of bands from *t* that disappeared between summer field seasons. Includes bands stallion that lost bands to another adult male and band stallions that died over winter.

Table A.1.3.6. Natal dispersal distances by age-class and sex for Sable Island feral horses between 2008 and 2010. Natal dispersals occurred outside of the summer seasons (i.e., winters of 2008−2009 and 2009−2010).

Age-class before natal dispersal	**Foal**		**Yearling**		**Young**	
	Female	Male	Female	Male	Female*	Male‡
Total dispersers	5	0	21	15	8	11
Destination⁴	FB	BG	FB	BG	FB	BG
Min distance (m)	1206.52	-	483.79	352.56	864.42	494.4985
Max distance (m)	5235.1	-	9887.86	8624.38	15125.59	7096.14
Average distance ± SD (m)	3572.11 ± 1545.87	-	3790.83 ± 2327.43	4002.75 ± 4002.75	4130.14 ± 4890.23	4167.97 ± 2310.30

Notes: *Three young females dispersed from natal bands during the summer season, one in each year. Distances are not included here.

‡Two young males dispersed from natal bands during the summer season, one in 2009 and one in 2010. Distances are not included here.

⁴Destination refers to band type into which dispersers moved, where FB = family band and BG = bachelor group.

All distances were calculated as the difference between median GPS locations for dispersers between consecutive years. Calculations were performed using the R Package aspace (Bui, Buliung, and Remmel 2010).

Table A.1.3.7. Dispersal distances by age-class and sex for Sable Island feral horses between 2008 and 2010. Dispersals occurred outside of the summer seasons (i.e., winters of 2008−2009 and 2009−2010).

Age-class before winter dispersal	**Foal**		**Yearling**		**Young**[ϕ]		**Adult**	
	Female*	Male*	Female*	Male	Female	Male	Female[ϯ]	Male
Total dispersers	13	15	8	3	30	5	40	0
Destination[ϕ]	FB	FB	FB	FB, BG	FB	BG	FB	-
Min distance (m)	385.82	206.28	368.91	871.57	267.83	153.48	230.89	-
Max distance (m)	16623.35	9550.32	8466.75	16623.35	9851.8	5166.19	16623.35	-
Average distance ± SD (m)	3602.68 ± 4555.92	2967.53 ± 4555.92	4212.56 ± 4050.65	8449.55 ± 7892.78	2836.09 ± 2880.8	2361.18 ± 2255.09	3823.04 ± 3664.93	-

Notes: *Female and male foals and female yearlings dispersed over winter with their mares

[ϕ]Young individuals dispersed over winter alone; distances do not include natal dispersal distances in Table A.1.3.6

[ϕ]Destination refers to band type into which dispersers moved, where FB = family band and BG = bachelor group.

All distances were calculated as the difference between median GPS locations for dispersers between consecutive years. Calculations were performed using the R Package aspace (Bui et al. 2010).

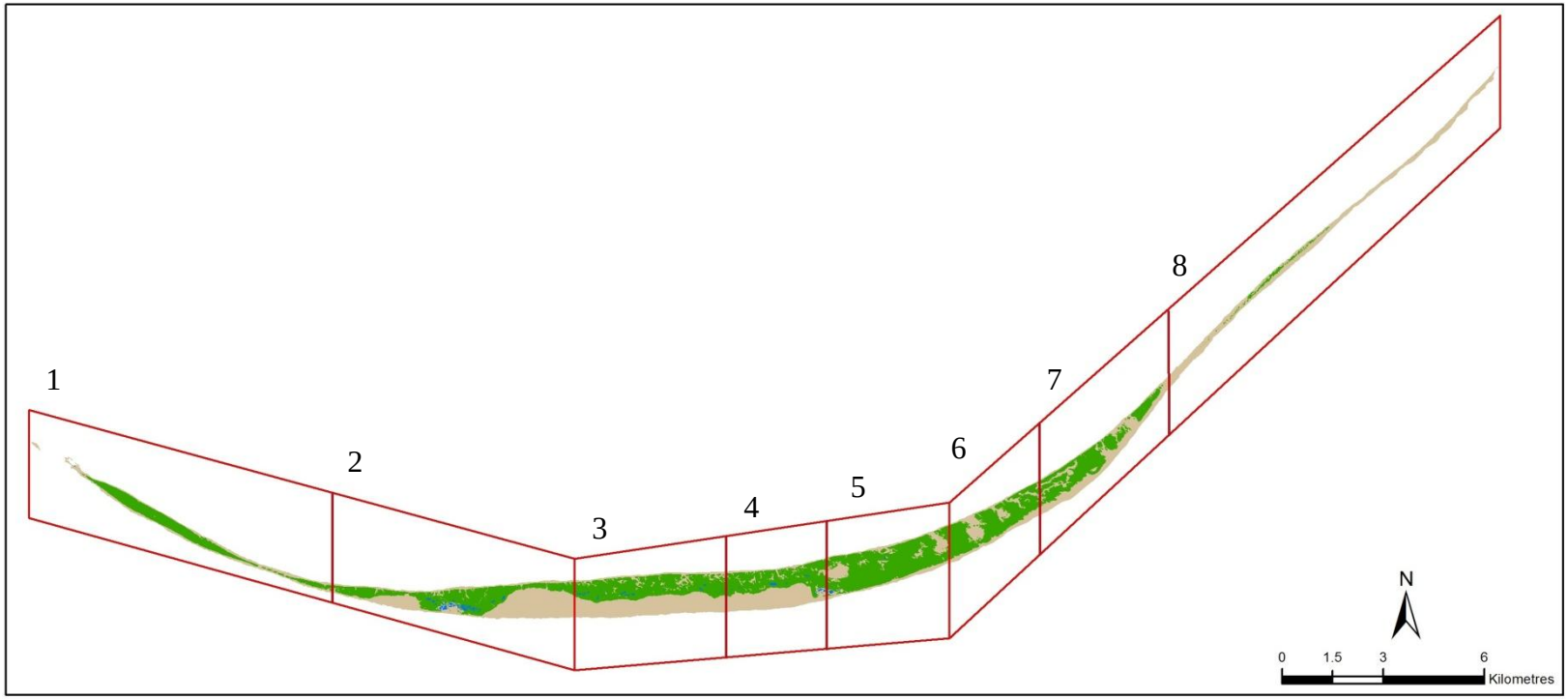

Figure A.1.4. Sable Island, Nova Scotia, Canada showing sampling areas 1 though 8 for my study. Areas were sampled on foot in a predetermined direction on each census day. Sequential areas were not sampled on consecutive days. GPS position data was collected for each horse observed within the boundaries of a sampling area on each census day. Map is modified from A. Muise 2011.

APPENDIX B: CHAPTER 2 SUPPORTING TABLES

Table B.2.3.1. Female horse annual vital rate estimates for each age class (2008−2009 and 2009−2010) including [¤]census estimated and [§]mean with [ϕ]95% CI age class survival and fertility rates.

2008−2009						
Vital rate			Census estimated	Bootstrap estimated		
		[Ψ]*n*		Lower limit	Mean	Upper limit
Survival	Foal	37	0.892	0.784	**0.893**	0.977
	Yearling	17	0.882	0.706	**0.886**	1.000
	2-year-old	34	1.000	1.000	**1.000**	1.000
	3-year-old	18	0.944	0.820	**0.943**	1.000
	Adult	84	0.917	0.848	**0.916**	0.975
Fertility	3-year-old	18	0.265	0	**0.269**	0.682
	Adult	84	0.215	0.152	**0.215**	0.279
2009−2010						
Vital rate			Census estimated	Bootstrap estimated		
		n		Lower limit	Mean	Upper limit
Survival	Foal	31	1.000	1.000	**1.000**	1.000
	Yearling	33	0.909	0.800	**0.909**	1.000
	2-year-old	15	0.933	0.786	**0.932**	1.000
	3-year-old	34	0.941	0.844	**0.942**	1.000
	Adult	94	0.904	0.865	**0.925**	0.973
Fertility	3-year-old	34	0.333	0.151	**0.330**	0.530
	Adult	94	0.313	0.200	**0.311**	0.431

Notes: [¤]Census estimated vital rate values were calculated from census observation of individual births and deaths that occurred during each year. [§]Mean vital rate values were estimated from 1000 resampled data sets for each year using bootstrap methods. [ϕ]95% CIs were calculated using the percentile method. [Ψ]*n* is the number alive post-birth pulse at time *t* for each year.

Table B.2.3.2. [‡]Deterministic and predicted [§]mean with [ϕ]95% CI values of λ during each year (2008−2009 and 2009−2010).

	Deterministic λ	Lower limit	Mean λ	Upper limit
2008−2009	1.065	1.008	1.065	1.123
2009−2010	1.108	1.061	1.117	1.170

Notes: [‡]Deterministic λ was estimated from a projection of census-calculated vital rates. [§]Mean λ was estimated from 1000 resampled matrices for each year using bootstrap methods. [ϕ]95% CIs were calculated using the percentile method. Calculations based on female portion of the population.

Table B.2.3.3. ‡Deterministic and predicted §mean and ϕ95% CIs stable age distribution for female horses during each year (2008−2009 and 2009−2010).

	2008−2009			
	Deterministic	Predicted		
		Lower limit	Mean	Upper limit
Foal	0.136	0.108	0.136	0.168
Yearling	0.114	0.091	0.114	0.137
2-year-old	0.095	0.074	0.094	0.115
3-year-old	0.089	0.071	0.089	0.106
Adult	0.566	0.487	0.567	0.649
	2009−2010			
	Deterministic	Predicted		
		Lower limit	Mean	Upper limit
Foal	0.163	0.130	0.161	0.189
Yearling	0.147	0.120	0.144	0.164
2-year-old	0.120	0.098	0.117	0.134
3-year-old	0.101	0.081	0.097	0.111
Adult	0.469	0.416	0.482	0.562

Notes: ‡Deterministic stable age distribution was estimated from a projection of census-calculated vital rates from each year. §Mean stable age distribution was estimated from 1000 resampled matrices for each year using bootstrap methods. ϕ95% CIs were calculated using the percentile method.

Table B.2.3.4. [‡]Deterministic and [§]mean and [ϕ]95% CI age class reproductive values for female horses during each year (2008−2009 and 2009−2010).

	2008−2009			
	Deterministic	Estimated		
		Lower limit	Mean	Upper limit
Foal	1.000	1.000	1.000	1.000
Yearling	1.194	1.075	1.196	1.352
2-year-old	1.442	1.193	1.450	1.805
3-year-old	1.535	1.236	1.544	1.929
Adult	1.451	1.041	1.466	1.987
	2009−2010			
	Deterministic	Estimated		
		Lower limit	Mean	Upper limit
Foal	1.000	1.000	1.000	1.000
Yearling	1.108	1.061	1.117	1.170
2-year-old	1.351	1.212	1.377	1.578
3-year-old	1.603	1.372	1.659	2.002
Adult	1.534	1.234	1.621	2.076

Notes: [‡]Deterministic reproductive values are estimated from a projection of census calculated vital rates from each year. [§]Mean reproductive values are estimated from 1000 resampled matrices for each year using bootstrap methods. [ϕ]95% CIs are calculated using the percentile method.

Table B.2.3.5. ‡Deterministic and §mean and ϕ95% CI age class specific vital rate elasticity values for female Sable Island horses during each year (2008−2009 and 2009−2010).

2008−2009					
Vital rate		Deterministic	Estimated		
			Lower limit	Mean	Upper limit
Survival	Foal	0.100	0.074	0.100	0.132
	Yearling	0.100	0.074	0.100	0.132
	2-year-old	0.100	0.074	0.100	0.132
	3-year-old	0.084	0.067	0.083	0.098
	Adult	0.517	0.385	0.518	0.631
Fertility	3-year-old	0.016	0	0.017	0.049
	Adult	0.084	0.067	0.083	0.098
2009−2010					
Vital rate		Deterministic	Estimated		
			Lower limit	Mean	Upper limit
Survival	Foal	0.119	0.093	0.113	0.133
	Yearling	0.119	0.093	0.113	0.133
	2-year-old	0.119	0.093	0.113	0.133
	3-year-old	0.097	0.078	0.093	0.105
	Adult	0.428	0.371	0.453	0.549
Fertility	3-year-old	0.022	0.008	0.021	0.037
	Adult	0.097	0.078	0.093	0.105

Notes: ‡Deterministic elasticity values are estimated from a projection of census calculated vital rates from each year. §Mean elasticity values are estimated from 1000 resampled matrices for each year using bootstrap methods. ϕ 95% CI are calculated using the percentile method.

APPENDIX C: CHAPTER 3 SUPPORTING FIGURES

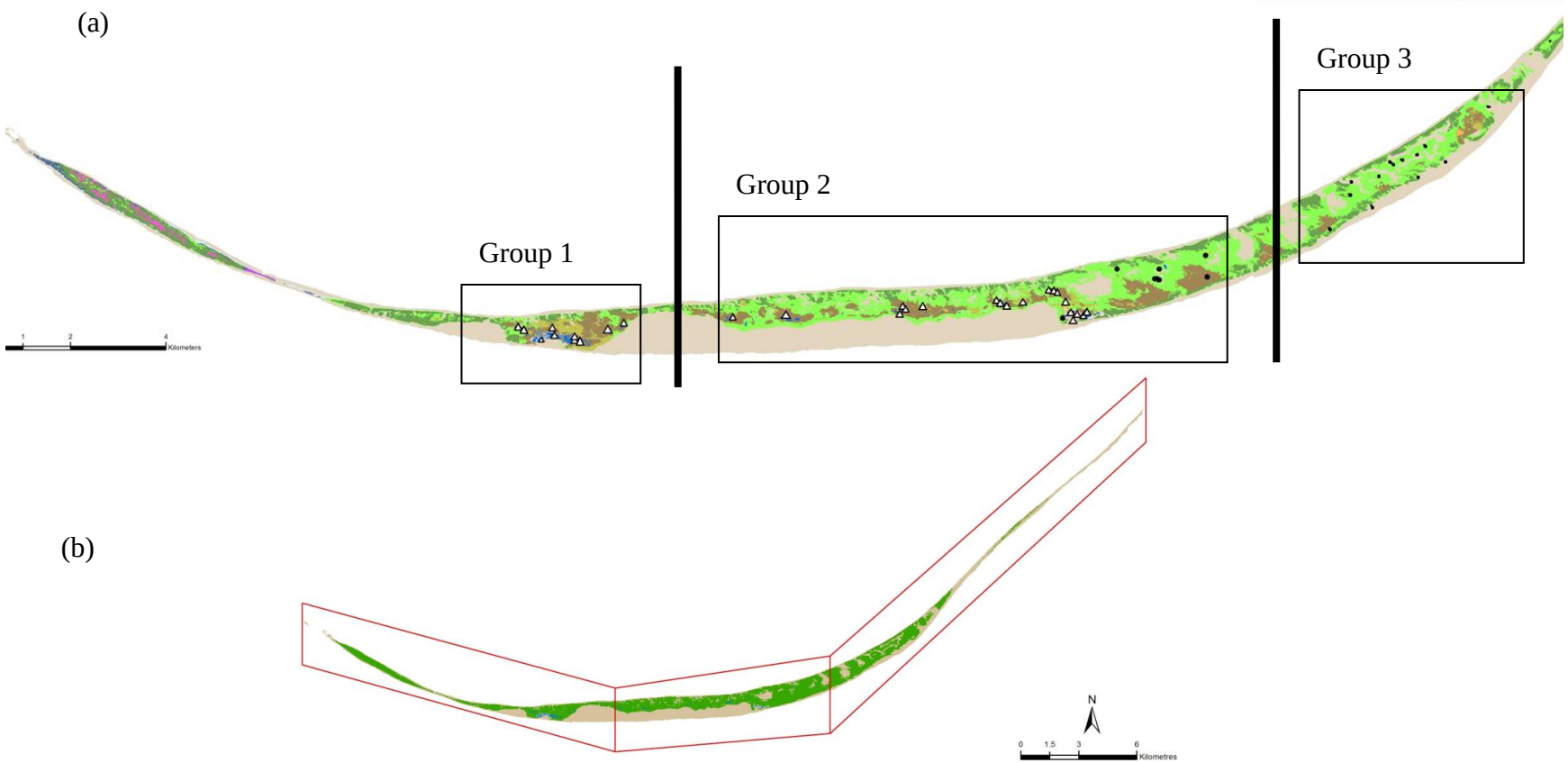

Figure C.3.2.1. (a) Three group HCA solution of longitudinal gradient in water resources (n = 122) on Sable Island. Vertical lines indicate area boundary divisions in (b) defined using GPS locations of females that used a particular water resource group. (b) Spatial population substructure showing boundaries of three areas defined by water resource groupings. Each area contains one water resource group and one population subunit. Maps are modified from A. Muise (AGRG 2011).

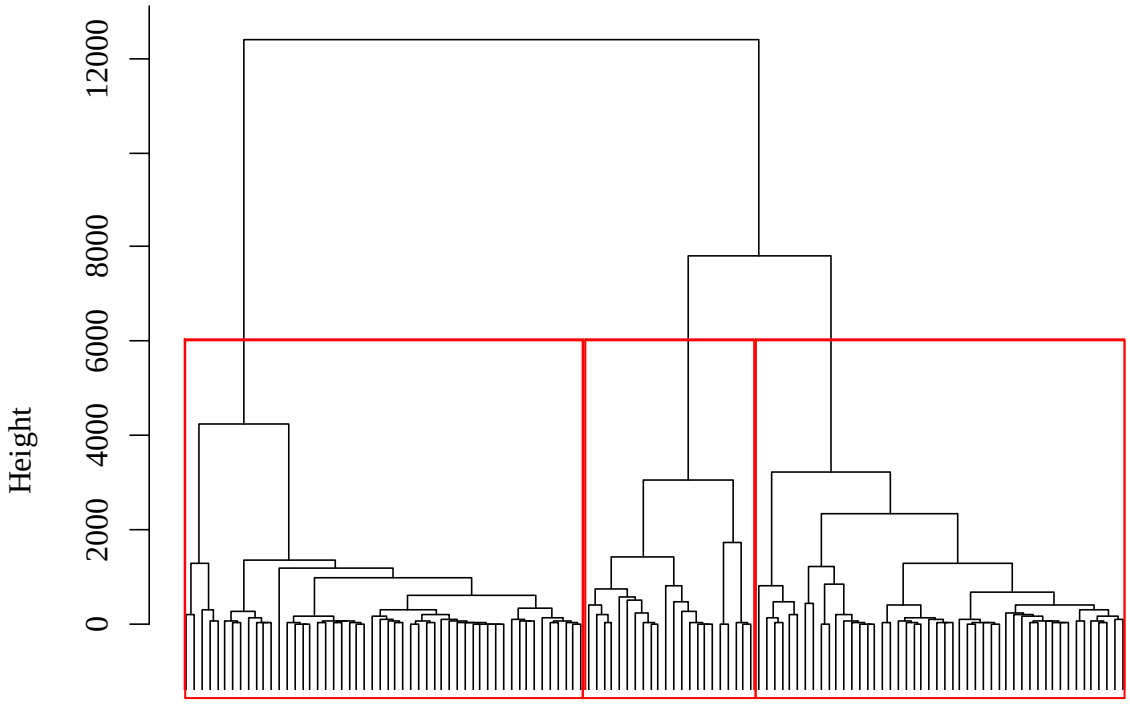

Figure C.3.3.1. Three-group HCA dendogram showing average clustering of Cartesian locations for water resources (ponds and dug holes, n = 122) on Sable Island, Nova Scotia. Water resource groupings were used to identify three neighbouring island areas; each area contains one cluster group (defined by rectangles). Each node represents a single water resource location.

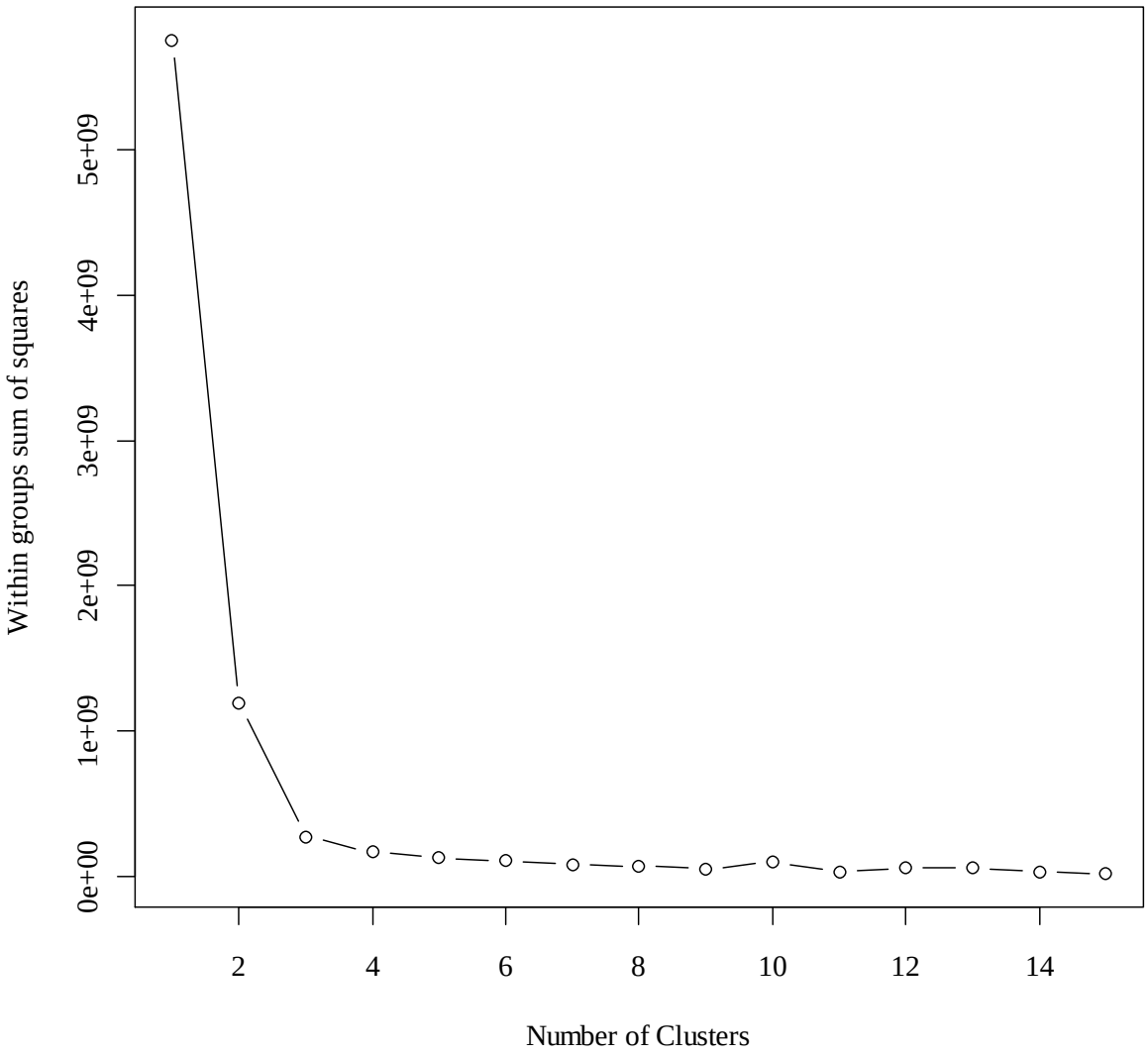

Figure C.3.3.2. *K*-means analysis indicating the appropriate number of group-clusters to select based on within groups sum of squares as a function of the number of clusters from a hierarchical clustering of water resources points (n = 122; Figure C.3.3.1). The first obvious bend indicates the appropriate number of group-clusters. The appropriate number of group-clusters is three.